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SOME RECENT INVESTIGATIONS IN SUGAR-BEET BREEDING

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(WITH FIFTY-ONE FIGURES)

Introduction

This investigation was made for the purpose of ascertaining certain facts and principles which have an important bearing upon methods of breeding. The introduction of more economical methods, based upon correlated characters or upon a better knowledge of scientific principles, would aid materially in the improvement of beets.

The efficiency of breeding methods depends largely upon the soundness of the scientific principles on which they are based. Unfortunately, many principles of breeding are still obscure, and even doubtful principles are employed as the basis of improving or originating a variety. Biologists who believe that improvement results from a gradual accumulation of small variations practice continuous selection, while those who adhere to a belief in improvement by the use of a few exceptional, prepotent individuals work with larger numbers and depend upon the isolation of mutations. In studying the effects of our own methods we have endeavored to determine whether improvement is accomplished through continuous selection, and also whether prepotent plants of exceptional quality occur within the limited range of our cultures.

A sugar-beet variety as ordinarily developed and maintained differs from a variety of other crops in that it consists of a number of

families which are preserved from generation to generation by continuous selection. Whenever a family shows deterioration it is discarded, but, as new families are annually added, the number composing the variety is not materially altered.

One of the most costly operations practiced in sugar-beet breeding is the determination of the so-called best roots, either for starting families or as representatives of families already established. This is accomplished by chemically analyzing the individual roots of each family and grading them upon the basis of size, shape, and percentage of sugar. The few best roots are saved to preserve the family and continue the process of improvement, while the remainder are thrown into a mixed lot and used for growing stock seed. A fairly good conception of the number of analyses made in commercial work of this kind is afforded by the records of a single European beet-seed company who analyze over 300,000 individual beets a year. The cost of making these analyses forms a large part of their operating expenses. Yet, aside from the theory that "like begets like," there seems to be little evidence that these highly selected roots are better for breeding purposes than the discards. It has apparently been assumed upon theoretical grounds that a high percentage of sugar tends to be transmitted, and therefore is the most important quality of a mother root without regard to the possibility of its being a fluctuating character and nowise indicative of the average quality of the plant's progeny.

Real differences between individuals and varieties are often obscured by variations caused by irregularities of the soil, which makes it difficult to distinguish hereditary differences from temporary differences and thus complicates the question of methods. The comparative efficiency of different methods has been treated somewhat in detail in another paper,[1] but the effect of environment on the behavior of consecutive check and progeny rows will be graphically illustrated here, as it presents a number of interesting phenomena which have an important bearing on the results of this investigation.

[1] A contribution to the use of checks and repeated plantings in variety tests.

While only a few of the beet breeders' problems have been outlined, they are fundamentally important and need investigation for the purpose of developing more economical methods.

Character of material employed

The material employed consisted of (1) an American variety of sugar-beets, known as Morrison's Kleinwanzleben; (2) an unnamed variety originated at Madison, Wisconsin, in 1912 by making selections from 11 foreign varieties and designated for convenience in reference as Madison Original Selections; (3) 5 South Dakota varieties bred for several years at Brookings, South Dakota; and (4) an old, well-established European variety, Kleinwanzleben's Original.

Morrison's Kleinwanzleben is composed of a large number of separate strains or families which have been preserved and improved by continuous selection. Ten years were devoted to this work at Fairfield, Washington, and 3 years at Madison, Wisconsin. The records obtained from these families and their individual components have furnished all the progeny row data not otherwise accounted for in the tables and figures.

Madison Original Selections are composed of beet families which originated from roots containing 18–26 per cent sugar. As no records of their performance were available until 1914, they have contributed few data to this paper.

The 5 South Dakota varieties used in our experiments at Brookings were originated by selecting rich roots from foreign stock and making subsequent tests and selections primarily upon the basis of a high percentage of sugar. About an equal number of roots were taken at random from each of these varieties to compile the data from this material, which are used in table I and graph A of fig. 51.

Kleinwanzleben's Original was the variety planted in the check rows. It is one of the most uniform, most highly bred, and most widely used varieties of sugar-beets on the market. The seed was taken from an unopened bag, sealed by the Rabethge & Giesecke Company at their plant, in order to increase the probability of

its all being grown in one locality under similar environmental conditions, and thoroughly mixed before being used, to enhance its uniformity.

Investigation

CONTROL OF CROSS-FERTILIZATION.—Undesirable cross-fertilization was avoided by planting the seed-beets of approximately equal qualities in isolated groups, a practice commonly followed in beet breeding. At Fairfield the quality was determined from the percentage of sugar, but at Madison a somewhat different method of classifying the roots was employed. As small beets are richer on the average than large beets, the regression coefficient was determined between weight and percentage of sugar and a correction made for size. Roots of equivalent value, as determined from both size and percentage of sugar, were then planted together at distances of 40–80 rods from other groups. However, at Brookings all the selected seed-beets of each variety were planted in a group and allowed to cross-fertilize with one another but not with beets of another group.

CHEMICAL CONTROL.—All the chemical work was done by experienced sugar chemists, the personnel consisting of JOSEPH F. REED at Fairfield, GUY YOUNGBERG at Brookings, and W. B. CLARK and assistants at Madison.

The sugar determinations of beet families were made at Fairfield by collecting roots at regular intervals in the row, grinding them to a fine pulp, and making composite analyses of the samples. A somewhat different method of procedure was followed at Madison. The quantity of sugar was first determined for each individual root and the sum of the quantities was then divided by the total weight of roots.

FIELD CONDITIONS UNDER WHICH THE MATERIAL WAS GROWN.—The experimental fields were fairly uniform with respect to soil-type, fertility, drainage, and previous cropping, and all field operations, as plowing, planting, thinning, cultivating, etc., were always performed in as short a time as circumstances would permit, in order to prevent the introduction of unequal factors.

SELECTION OF FOUNDATION STOCK.—The choosing of a variety as foundation stock often has as much to do with the improvement

of a crop as subsequent selections. Sugar-beet varieties are seldom distinguishable from one another morphologically, however, and as they have nearly the same descent, some doubt may be expressed regarding the existence of real variety differences. In order to determine the truth of this hypothesis, 78 families of Morrison's Kleinwanzleben,[2] which made the best records for percentage and yield of sugar at Madison in 1912, and 52 families of Madison Original Selections were used in a comparative merit test in 1914.

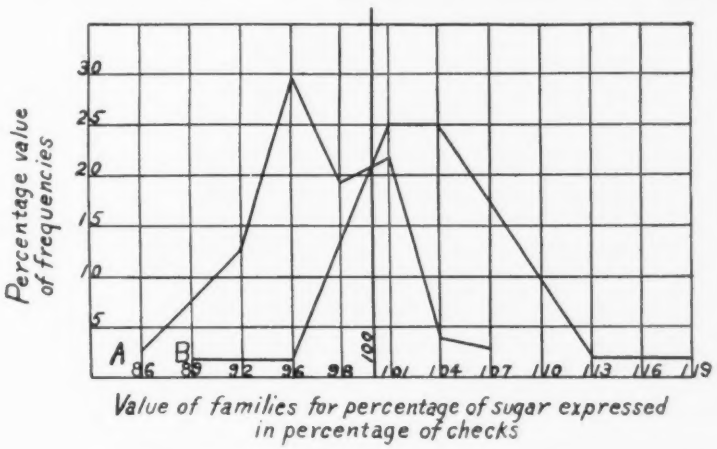

FIG. 1—Comparison of two kinds of sugar-beet material used as foundation stock.

A progeny row of each family (seed of a single beet) was planted between two check rows of Kleinwanzleben's Original. When the beets were harvested, each progeny row was compared with the average of its two contiguous checks by giving the latter a value of 100 and computing the value of the progeny row upon this basis. In fig. 1 the vertical line represents the values of the check rows for percentage of sugar; the frequency polygons *A* and *B*, Morrison's Kleinwanzleben and Madison Original Selections, respectively. The frequencies were reduced to percentages by

[2] In 1912 these families were grown from seed of Fairfield roots containing 20–22 per cent sugar.

dividing each class by the total number of variates in the population; hence the graphs are comparable.

Fig. 1 shows the superiority of Madison Original Selections over Morrison's Kleinwanzleben at Madison, where the percentage of sugar is normally low and a higher percentage is the chief desideratum. Hence the foreign varieties from which the Madison Original Selections were made are better as foundation stock at Madison than the variety Morrison's Kleinwanzleben. One or two plantings of each variety would hardly suffice to show this difference, but the large number of replications used were sufficient to establish it with a fair degree of certainty.

Morrison's Kleinwanzleben has been selected for a high yield of sugar, and in tests with foreign varieties in several different localities in the United States it has usually stood preeminent in this respect. In a 5 years' test at Fairfield, Washington, where it was bred for 10 years, it was equal to Kleinwanzleben's Original and better than 11 other varieties in percentage of sugar and ranked first in yield of sugar. At Madison, however, it is not well adapted to the breeders' needs as foundation stock. Although it was superior to Kleinwanzleben's Original in yield of sugar in 1913 (cf. fig. 30), it was inferior to it in 1912. It was relatively low in percentage of sugar in comparison to the checks (KWO) in 1912, and continued to maintain this position in its second year's test after all the supposedly poor families had been eliminated.

SELECTION OF MOTHER ROOTS.—The selection of mother roots for the purpose of starting a new family of beets or improving one already established is usually made upon the basis of size, shape, percentage of sugar, and relative freedom from mineral substances which interfere with the extraction of sugar. The coefficient of purity is not usually determined for breeding purposes, however, as only roots containing a high percentage of sugar are saved and they are almost invariably characterized by high purity. As size and shape are distinguished by physical selection, percentage of sugar is the only character determined chemically.

VARIABILITY OF MATERIAL FROM WHICH MOTHER ROOTS WERE SELECTED.—The variability of beet roots in percentage and quantity of sugar is ample for selection, as may be seen in table I.

The average variability of the roots as shown by the standard deviations was 1.25–1.59 per cent sugar and 19.28–37.99 grams of sugar. Measured by the coefficient of variability, this amounts to 6–12 per cent of the mean for percentage of sugar and 18–50 per cent for quantity of sugar, which are fairly large differences for averages.

TABLE I

VARIABILITY OF SUGAR-BEET ROOTS IN PERCENTAGE AND QUANTITY OF SUGAR

Station	Year	Number of roots analyzed	Mean	Standard deviation	Coefficient of variability
Percentage of sugar in roots					
Fairfield.....	1907	230	20.15±0.056	1.26±0.039	6.25
"	1909	400	20.37±0.048	1.47±0.035	7.22
"	1910	400	17.34±0.044	1.31±0.031	7.55
"	1910	400	18.76±0.042	1.25±0.029	6.66
Brookings.....	1911	3784	17.67±0.017	1.59±0.012	8.99
Madison.....	1912	500	12.86±0.047	1.55±0.033	12.06
"	1913	500	14.24±0.041	1.35±0.029	9.46
Quantity of sugar per root in grams					
Madison.....	1912	500	98.46±1.146	37.99±0.810	38.58
"	1913	500	54.02±0.807	26.76±0.570	49.53
Fairfield.....	1910	126	104.61±1.191	19.85±0.850	18.97
"	1910	147	104.90±1.077	19.28±0.770	18.38
"	1909	231	113.68±1.134	25.43±0.790	22.37
Brookings.....	1911	3784	79.87±0.266	23.94±0.186	29.97

The range of variation for percentage of sugar in individual beets is not shown in table I, but varies ordinarily from about 8 to 24. Small, immature beets frequently contain less than 8 per cent sugar, and occasionally a root is found which contains more than 24 per cent. We found one beet at Madison which showed 26 per cent sugar in 2 separate analyses. Another small root, so small in fact that it had to be bored lengthwise through the center to obtain a sample of pulp, contained 30 per cent sugar.

RELATIONSHIPS BETWEEN A FEW COMMONLY DETERMINED CHARACTERS OF THE ROOT AND ITS YIELD OF SEED.—A knowledge of the relationship of such characters as root weight and percentage of sugar to seed production is essential to intelligent selection. Very

frequently beet roots are separated into selects and discards on small differences. A satisfactory method of predicting seed yields would not only alter these results but would furnish a means of obtaining sufficient seed to make several plantings of each family.

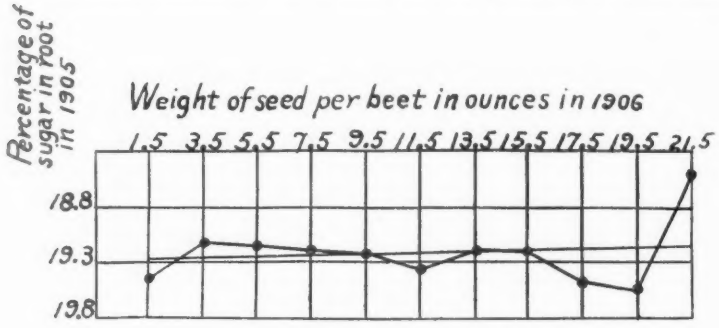

FIG. 2.—To accompany table II

Tables II–XI (summarized on p. 463) and figs. 2–11 show the relationships which obtain between these characters. Some of the tables show slight irregularities, but they are not sufficient to invalidate the results. The effects of the irregularities may be seen in

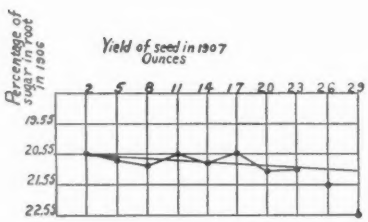

FIG. 3.—To accompany table III

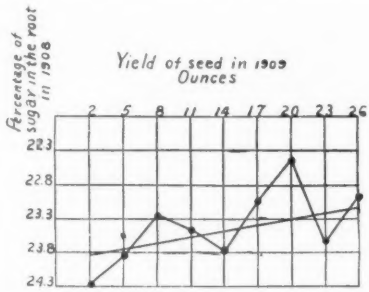

FIG. 4.—To accompany table IV

the deviation of the dots representing the empirical means of the separate classes from the straight line regressions. The divergence is not marked except where the numbers are small. Moreover, the general trends of the broken lines connecting the empirical means agree fairly well in direction with the straight line regres-

sions. The distributions are fairly regular, therefore, and the coefficients are probably reliable.

When due consideration is given to probable errors,[3] the coefficients show no correlation between weight, percentage of

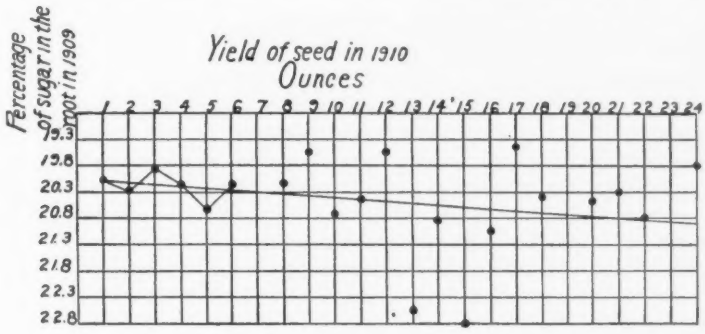

FIG. 5.—To accompany table V

sugar, or quantity of sugar of the seed beet and its yield of seed. This refers to beets of ordinary sizes such as are grown for factory use. Very small beets, 0.5–2 inches in diameter (stecklings), form a little less seed per plant than large roots, although they grow to

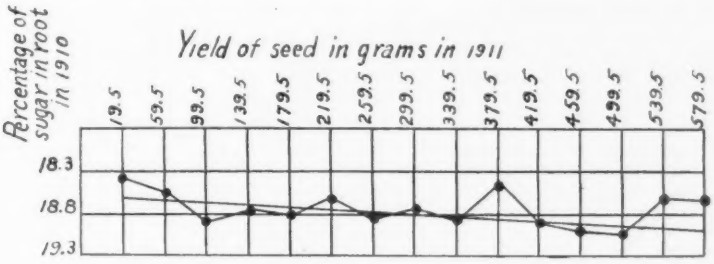

FIG. 6.—To accompany table VI

nearly normal size while producing seed. There is little doubt regarding the absence of correlation between these characters, as the tables cover a number of years and the results all lead to the

[3] The biometrical constant should exceed 3–4 times the probable error to have significance.

same conclusion. However, BARTOS[4] has found that seed production decreases as percentage of sugar increases. His average differences are only 3.3 and 8.6 per cent, however, and in the absence of probable errors we have no means of determining whether they bear any significance.

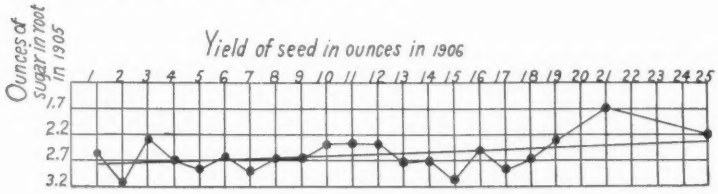

FIG. 7.—To accompany table VII

If percentage of sugar were negatively correlated with seed yield, as BARTOS believes, it would constitute an undesirable relationship. Even positive correlation between percentage of sugar and seed yield, or between weight of root and seed yield, would form a less desirable relationship than the absence of correlation, as high percentage is correlated with low yield and high tonnage with low purity. Maximum sugar production is dependent upon both percentage and tonnage, and consequently cannot run to either extreme. Positive correlation between extractable sugar and seed yield, however, would constitute a very desirable relationship, as selection for maximum sugar production would also tend to increase the seed yield.

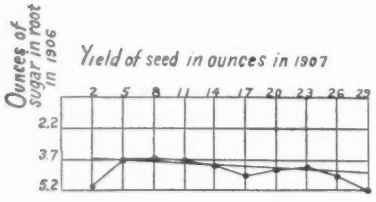

FIG. 8.—To accompany table VIII

RELATIONSHIP BETWEEN A ROOT'S YIELD OF SEED AND THE PERCENTAGE OF SUGAR IN ITS PROGENY.—No distinction between individual sugar-beet plants can safely be made in the seed generation until we learn what relationship exists between a root's yield of seed and the average sugar-producing capacity of its progeny.

[4] BARTOS, V., Je zucherhaltiger die Rübensorte ist desto kleinere Samenfruchtbarkeit hat sie. Cukrovarnicke Listy, December, 1908; rev. Bl. Zucherrübenbau 16: 93. 1909.

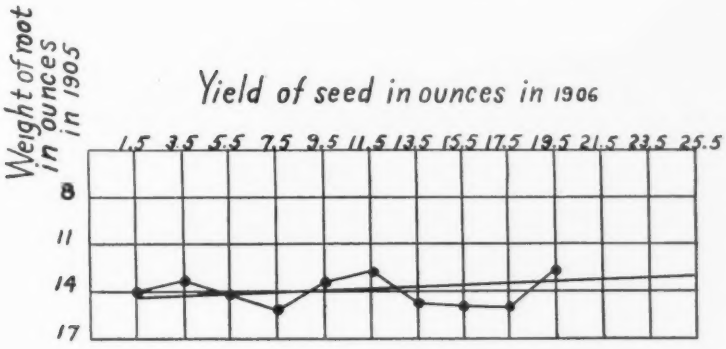

FIG. 9.—To accompany table IX

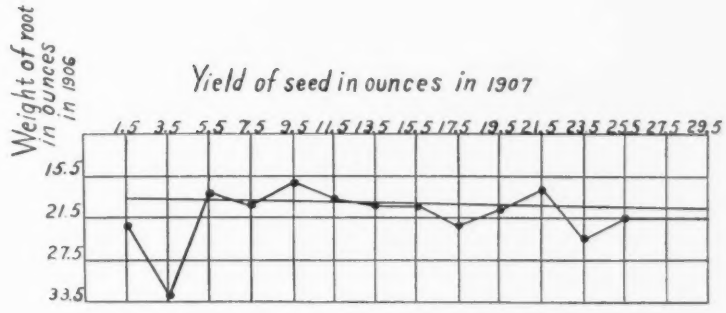

FIG. 10.—To accompany table X

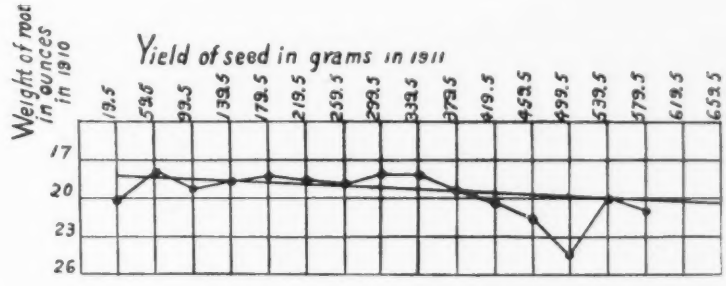

FIG. 11.—To accompany table XI

Tables XII and XIII disclose this relationship. In the experiment from which the records were obtained, the seed of each plant was

TABLE XII

RELATIONSHIP BETWEEN A BEET'S YIELD OF SEED AND THE AVERAGE PERCENTAGE OF SUGAR IN ITS PROGENY; YIELD OF SEED IN 1912

Centers of percentage of sugar classes of 0.5 per cent range in progeny of 1913	Centers of weight classes of 25 gm. range											
	162.5	187.5	212.5	237.5	262.5	287.5	312.5	337.5	362.5	387.5	412.5	Totals
13.0	1*	1	0	0	0	0	0	0	0	0	0	2
13.5	4	1	0	1	0	0	0	0	0	0	0	6
14.0	3	1	1	3	3	0	0	1	0	0	0	12
14.5	9	5	1	1	0	2	0	0	0	0	0	18
15.0	6	2	4	2	1	0	0	0	0	0	0	15
15.5	10	9	5	4	1	0	0	0	0	0	0	29
16.0	3	8	2	3	0	0	1	1	0	0	1	19
16.5	8	3	3	2	1	0	0	0	0	0	0	17
17.0	3	1	0	0	0	0	0	0	0	0	0	4
17.5	1	1	0	0	1	0	0	0	0	0	0	3
Totals	48	32	16	16	7	2	1	2	0	0	1	125

Mean yield of seed, 198.5 gm.; mean percentage of sugar, 15.32; standard deviation in yield of seed, 43.405 gm.; standard deviation in percentage of sugar, 0.996; coefficient of correlation, −0.013.

* Number of beets in the classes in 1912.

TABLE XIII

RELATIONSHIP BETWEEN A BEET'S YIELD OF SEED AND THE AVERAGE VALUE OF ITS PROGENY FOR PERCENTAGE OF SUGAR EXPRESSED IN PERCENTAGE OF THE CHECKS; YIELD OF SEED IN 1912

Percentage of sugar in progeny divided by percentage of sugar in checks in 1913	Centers of weight classes of 25 gm. range											
	162.5	187.5	212.5	237.5	262.5	287.5	312.5	337.5	362.5	387.5	412.5	Totals
83.5	0	1	0	0	0	0	0	0	0	0	0	1
85.5	3*	0	3	0	0	0	0	0	0	0	0	6
87.5	4	7	0	3	1	0	0	0	0	0	0	15
89.5	6	6	3	0	1	0	0	2	0	0	1	19
91.5	8	6	2	4	1	0	1	0	0	0	0	22
93.5	13	4	4	2	2	1	0	0	0	0	0	26
95.5	5	3	2	2	1	0	0	0	0	0	0	13
97.5	3	2	1	4	0	0	0	0	0	0	0	10
99.5	3	1	1	0	1	1	0	0	0	0	0	7
101.5	3	2	0	1	0	0	0	0	0	0	0	6
Totals	48	32	16	16	7	2	1	2	0	0	1	125

Mean yield of seed, 198.5 gm.; mean value of progeny, 92.6 per cent of percentage of sugar contained in their checks; standard deviation in yield of seed, 43.405 gm.; standard deviation in value of progeny 14.07 per cent of percentage of sugar contained in their checks; coefficient of correlation, −0.010.

* Number of beets which produced seed in 1912 and progeny in 1913.

sown in a progeny row between 2 check rows of Kleinwanzleben's Original. The relationship between seed yield and percentage of sugar was determined from the data both with and without the use of checks. In table XII actual percentages of sugar are recorded in the horizontal columns, but in table XIII the values occupying these columns were obtained by dividing the percentage of sugar of each progeny row by the average percentage of sugar of its 2 contiguous checks. As the 2 tables were compiled from the same data they are alike, except that table XII shows the relationship between seed yield and percentage of sugar when no checks were used, and table XIII when every alternate row was employed as a check.

The tables show no correlation between a beet's yield of seed and the average percentage of sugar in its progeny. The application of this fact to sugar-beet breeding is obvious, as extensive selections may be made for freer seed production without danger of sugar deterioration. Moreover, it affords an opportunity to reverse the order of selection by making the chief eliminations in the seed generation and thus greatly reduce the amount of chemical work and increase the effectiveness of the working funds.

TRANSMISSION OF SELECTED QUALITIES OF MOTHER ROOTS.—Mother roots are selected chiefly on the basis of size, shape, and percentage of sugar, because these qualities are desired in the progeny and there is a popular belief that they are inherited, but we really know very little regarding the transmission of such characters. In the early period of beet breeding they appeared to improve through selection, but this was at a time when the material was very variable and full of distinct physiological species. Improvement probably resulted from the isolation of these species, although the selections were made with a view to improving the characters. Today it is quite different. The poorer physiological species have gradually been eliminated and all varieties are now much alike. Moreover, such root characters as size and percentage of sugar—and incidentally this includes total sugar content—are markedly influenced by the environment. Consequently large fluctuations occur which are indistinguishable from hereditary differences. The fluctuations probably characterize the supposedly

best beets, in which case the cost of analyzing mother roots is an absolute waste of money. Tables XIV–XXV (summarized on p. 463) and figs. 12–23 show the extent to which we have found

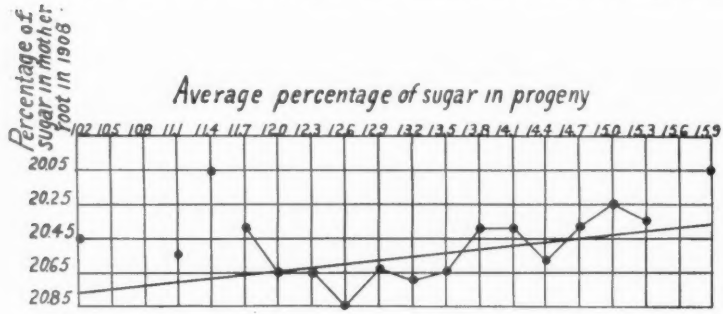

FIG. 12.—To accompany table XIV

weight, percentage of sugar, and total sugar content of the root to be transmitted to the progeny.

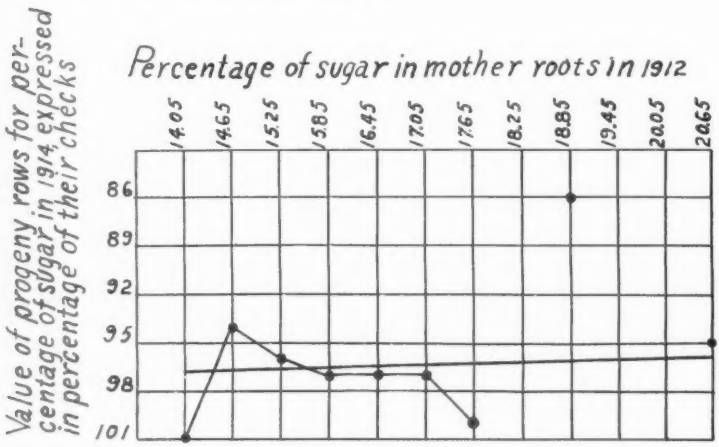

FIG. 13.—To accompany table XV

The results show no correlation between percentage of sugar, weight, or sugar content of the root and the average value of the same quality in its progeny. There is no constant relationship

between the weight of the mother root and the average percentage of sugar or the average sugar content of its progeny roots. Moreover, exceptionally good roots transmit no different qualities than

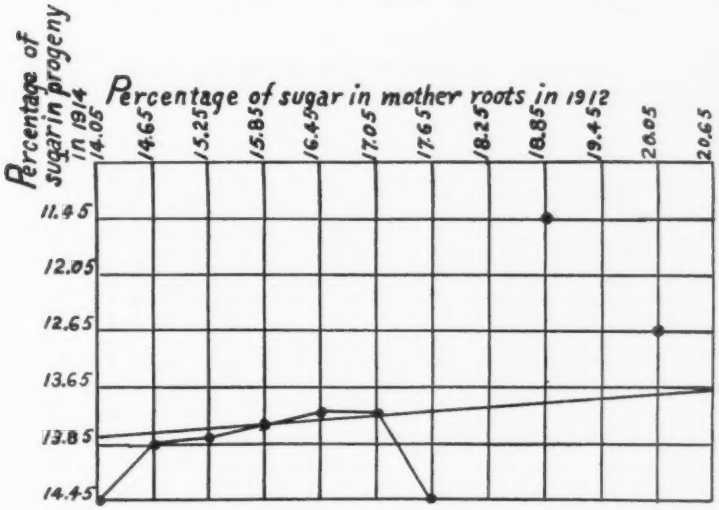

FIG. 14.—To accompany table XVI

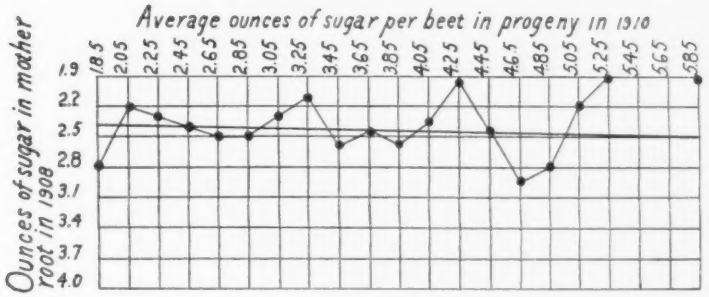

FIG. 15.—To accompany table XVII

do average roots. In fact, the poorest roots made as good progeny records as the best roots. While cross-fertilization may have had an equalizing tendency upon the qualities, real differences could hardly be eliminated in one generation, as both good and

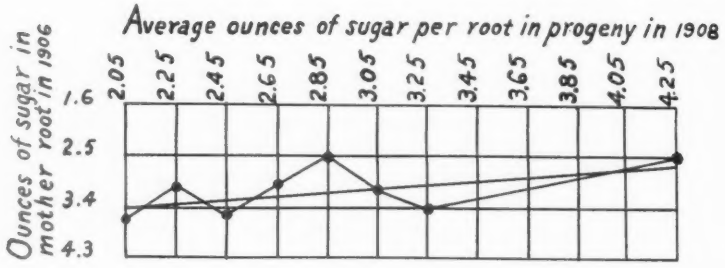

FIG. 16.—To accompany table XVIII

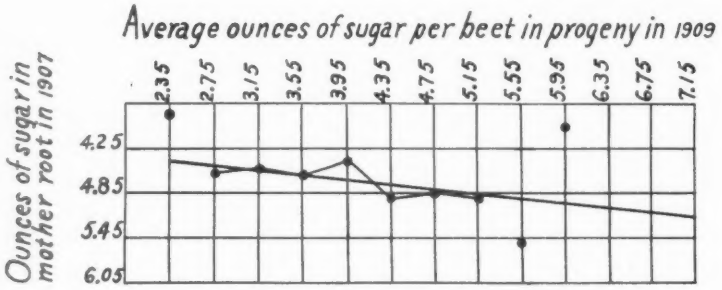

FIG. 17.—To accompany table XIX

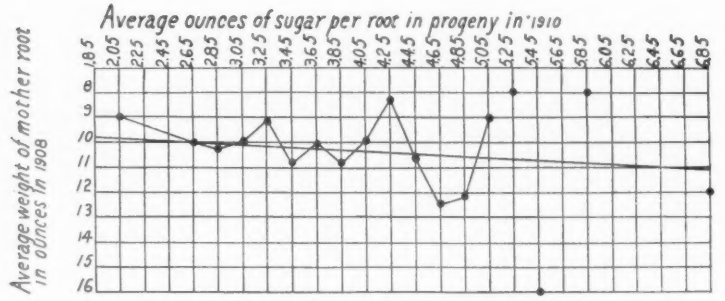

FIG. 18.—To accompany table XX

poor plants would receive pollen of equal average quality, and hence the better mothers should produce the better average progeny. Moreover, the fact that insects visit several flowers before leaving a plant probably causes a considerable percentage of selfing, even

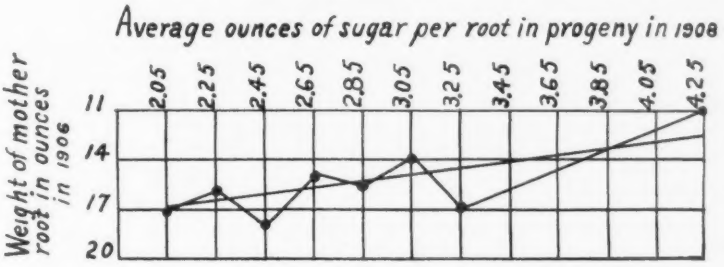

FIG. 19.—To accompany table XXI

though the plant may prefer foreign pollen. If hereditary differences occur in mother roots and are transmitted to their progeny, they are certainly obscured by fluctuations caused by irregularities of the soil, which influence the qualities of both mother root and progeny, and thus baffle the breeder's attempt to discover real differences. By planting each family 10–20 times and using a considerable number of checks it may be possible to distinguish hereditary differences between their progeny, but this would hardly apply to mother roots. In fact, these results seem to condemn the customary practice of selecting mother roots by current physical and chemical means. Taking roots at random would certainly be much cheaper and apparently fully as effective.

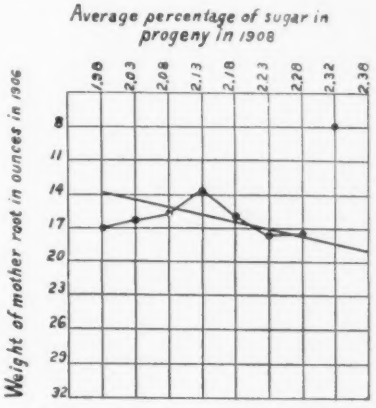

FIG. 20.—To accompany table XXII

SELECTION OF FAMILIES.—Sugar-beet families are selected upon the basis of percentage and yield of sugar. Extreme selection in either direction is avoided, as a maximum yield of sugar is usually associated with a moderately high percentage of sugar, while an

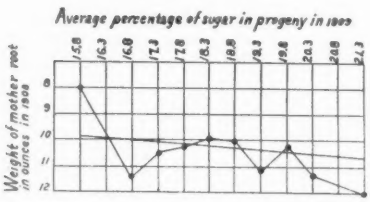

FIG. 21.—To accompany table XXIII

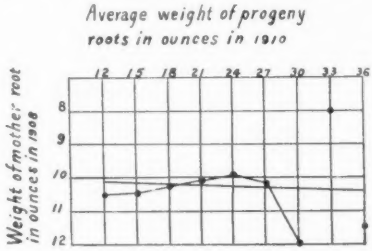

FIG. 22.—To accompany table XXIV

extremely high percentage is generally indicative of a low tonnage. As the presence of inorganic salts lowers the percentage and prevents the extraction of about an equal quantity of sugar, selection for extractable sugar is the most ideal method to employ, but it has

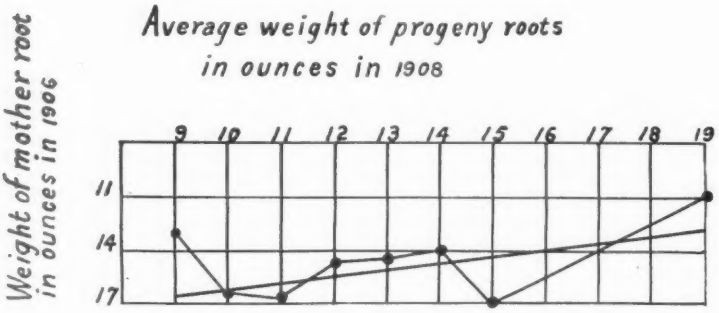

FIG. 23.—To accompany table XXV

the disadvantage that additional chemical work is required to determine the coefficients of purity. Relative merits, therefore, are more economically determined from the percentage of sugar and total yield of sugar.

VARIABILITY OF PROGENY ROWS.—Progeny rows show considerable variation even when the stand of beets is compara-

tively uniform. The coefficients of variability presented in table XXVI were determined from 173 beet families of Morrison's Kleinwanzleben grown at Madison, Wisconsin, in progeny rows of 40–50 beets each in 1912, and from 98 families of the same stock grown under similar conditions at Madison in 1913.

TABLE XXVI

VARIABILITY OF SUGAR-BEET FAMILIES

Percentage of sugar

Year	Mean	Standard deviation	Coefficient of variability
1912.....	13.60±0.068	0.998±0.048	7.34
1913.....	15.41±0.058	1.009±0.041	6.54

Yield of sugar per row

Year	Mean (gm.)	Standard deviation (gm.)	Coefficient of variability
1912.....	4276.26±32.67	637.08±23.00	14.90
1913.....	2074.70±19.64	288.18±13.88	13.89

The average variability of progeny rows expressed in percentage of the mean was 6.54–7.34 for percentage of sugar, and 13.89–14.90 for yield of sugar. Although these constants are smaller than the coefficients obtained for individual beets of the same families, 9.46–12.06 and 38.58–49.53 for percentage and yield respectively, they are fairly large for averages.

The range for percentage and yield is not shown in the table, but rows containing 80–100 per cent stand varied from 10.1 to 15.7 in percentage of sugar in 1912, and from 13.2 to 17.4 in 1913; while the extreme yields for the same periods were 2383–5654 and 1423–2746 gm. respectively. Such differences certainly offer ample opportunity for selection.

EFFECT OF SOIL IRREGULARITIES UPON THE VARIABILITY OF BEET FAMILIES.—This was determined from the records of our sugar-beet breeding experiments in which progeny rows and check rows were planted alternately.

As family differences exhibited in field tests may be due to several causes, some method had to be adopted for studying soil

effects that would eliminate such factors as family hereditary differences, and the possible use of too small a number of plants to form a representative sample of the family. This was accomplished by plotting the mean values of consecutive progeny rows

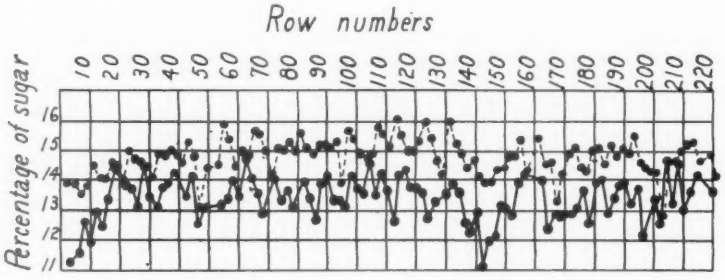

FIG. 24.—Effect of soil irregularities on percentage of sugar of check and progeny rows, strip 1, Madison, 1912; solid line indicates progeny rows; broken line, check rows.

for percentage and yield of sugar in the same order as the rows occurred in the field. Family differences in percentage or yield of sugar which show regular progression in direction are assumed

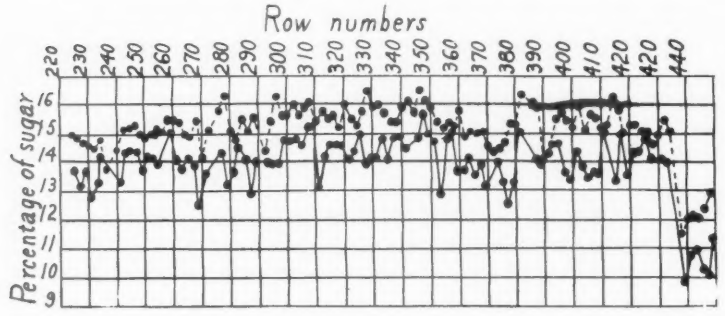

FIG. 25.—Effect of soil irregularities on percentage of sugar of check and progeny rows, strip 2, Madison, 1912; solid line indicates progeny rows; broken line, check rows.

to be due to the inequalities of the soil, while differences which show no such regularity may be due either to local soil disturbances or to other causes. A check on the results of the foregoing method is afforded by plotting the mean values of progeny rows of contigu-

ous strips whose row ends abut, and noting whether the same relative parts of the different strips show the same irregularities. Another check better adapted to show local soil irregularities and more generally applicable consists in plotting the mean values of

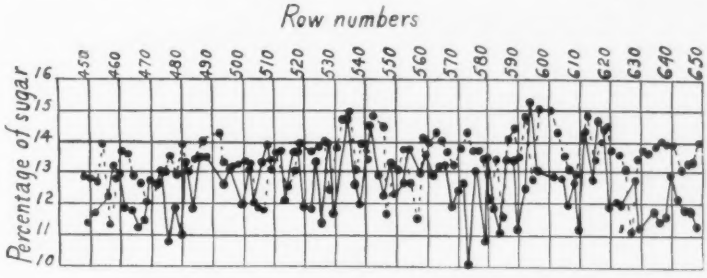

FIG. 26.—Effect of soil irregularities on percentage of sugar of check and progeny rows, strip 3, Madison, 1912; solid line indicates progeny rows; broken line, check rows.

the check rows in regular order. If these values show the same progressions as the means of the progeny rows, the effects are doubtless due to irregularities of the soil.

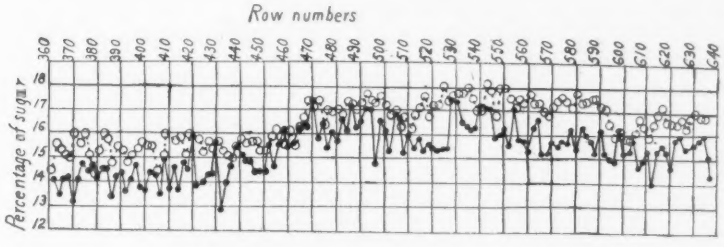

FIG. 27.—Effect of soil irregularities on percentage of sugar of check and progeny rows, Madison, 1913; solid line indicates progeny rows; broken line, check rows.

In the accompanying graphs, figs. 24–29 show the mean percentage of sugar, and fig. 30 the mean yield of sugar of consecutive progeny rows and check rows. Figs. 24–26 represent 3 contiguous strips of the same field which meet at their row ends. Strips 1 and 2 were planted on the same date, but strip 3 was plowed up and replanted on account of a poor stand. Consequently, the beets

in strip 3 were not fully mature when harvested, as may be seen from their low percentage of sugar. The row numbers run consecutively, but only every tenth row is numbered in the figures.

The regularity in the trend of mean percentages of sugar in figs. 24–29 and of mean yields of sugar in fig. 30 shows that soil irregularities have a marked influence on the behavior of progeny rows and check rows. The close agreement of progeny rows and check rows is remarkable and shows the advantage of employing

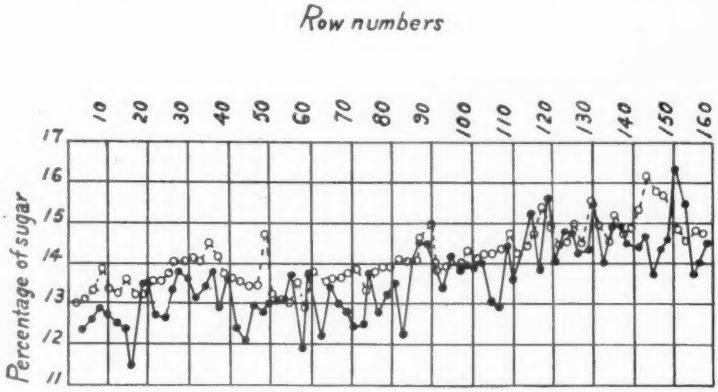

FIG. 28.—Effect of soil irregularities on percentage of sugar of check and progeny rows, Madison, 1914; solid line indicates progeny rows (Morrison's Kleinwanzleben); broken line, check rows.

frequent checks over the use of the mean value of the progeny rows as a standard of comparison. If the graphs are examined closely, it will be noted that a progeny row and its check rows frequently vary in opposite directions, although following the general trend of neighboring rows. Occasionally these peculiarities may be due to the hereditary nature of the progeny row of beets, but more frequently they are the result of local soil disturbances, as may be seen from similar deviations of check rows from their general trend. On the average the consecutive deviations of check rows from their trends appear smaller than the corresponding deviations of the progeny rows. Hence real differences between progeny rows may exist, but they are small in comparison with the fluctuations.

The only practical method of overcoming the effects of sudden soil disturbances is the employment of replications. Repeated plantings of each family between check rows of a standard variety will give a more reliable means of comparison than a single planting.

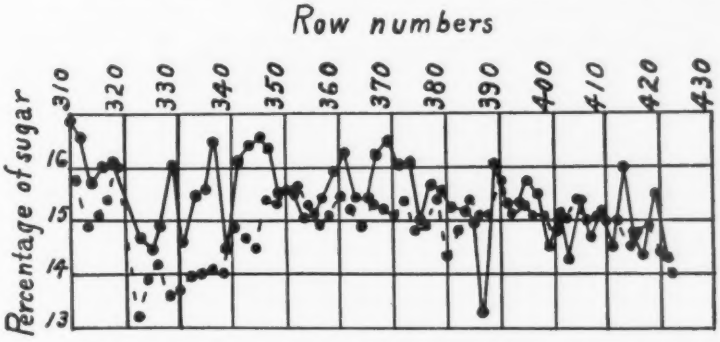

FIG. 29.—Effect of soil irregularities on percentage of sugar of check and progeny rows, Madison, 1914; solid line indicates progeny rows (Madison Original Selections); broken line, check rows.

A decided change in the direction of the graphs is shown in rows 132–155, 346–382, and 595–612 of the 3 contiguous strips in figs. 24–26. This difference is not due to the presence of a dead

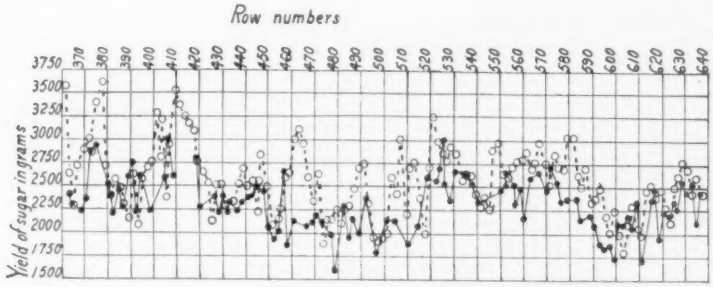

FIG. 30.—Effect of soil irregularities on yield of sugar of check and progeny rows, Madison, 1913; solid line indicates progeny rows; broken line, check rows.

furrow or back furrow, as no such areas were included in the experiment. Moreover, the disturbance covers an area 30–40 ft. wide in strips 1 and 2. The remarkable drops in percentage of

sugar in rows 435–449 has not been accounted for. These rows belong to strip 2, as indicated in the figure, and not to strip 3, as might be inferred from their behavior.

A variation of 2 per cent sugar occurs between different parts of the same field, as shown in figs. 27 and 28. These local differences are not limited to the progeny rows, but appear also in the check rows, and hence cannot be attributed to accidental groupings of good or poor families. The yields exhibited in fig. 30 are fully as variable as the percentages and show striking progressions with frequent changes in direction.

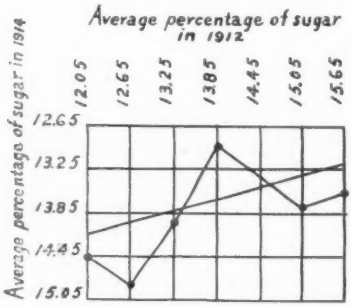

FIG. 31.—To accompany table XXVII

TRANSMISSION OF QUALITIES EXHIBITED BY SELECTED FAMILIES.—Average root weight and average percentage of sugar are the chief factors which determine the relative merits of sugar-beet

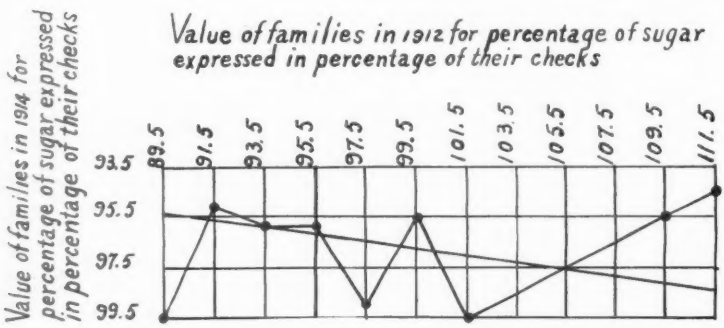

FIG. 32.—To accompany table XXVIII

families grown under uniform spacing, as they represent both yield and quality; but since these characters are very easily modified by the environment, it is doubtful whether real family differences are ordinarily distinguishable. In fact, fluctuations appearing under field conditions probably exceed the real differ-

ences between families. Tables XXVII–XXXII (summarized on p. 464) and figs. 31–36 show whether such family characters as percentage of sugar, average root weight, and average sugar content of the root are transmitted from generation to generation. Tables XXVII and XXVIII were compiled from the same data.

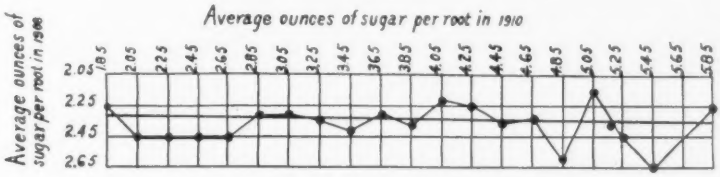

FIG. 33.—To accompany table XXIX

Table XXVII shows the relationship between the average percentages of sugar in two consecutive generations of beet families when no checks were used; table XXVIII shows the same relationship when every alternate row was employed as a check, and the value of each family was determined by dividing its percentage of sugar by the average percentage of sugar of its two contiguous checks. The families used in compiling data for tables XXIX–XXXII were planted without checks.

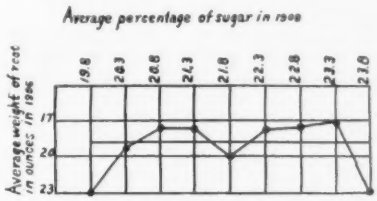

FIG. 34.—To accompany table XXX

No correlation is shown in tables XXVII and XXVIII between the percentages of sugar in two consecutive generations of a beet family. Even when every alternate row was planted as a check to offset the effects of the inequalities of the soil, the coefficient of correlation was only 0.089, while its probable error was 0.076.

Tables XXIX–XXXII furnish no evidence of correlation between average root weight or average quantity of sugar in successive generations, nor between average root weight in one generation and percentage of sugar in the following generation.

As a root's weight is negatively correlated with its percentage of sugar and positively correlated with its total sugar content, an absence of correlation between one pair of characters in tables XXVII–XXXII would signify a lack of correlation between each

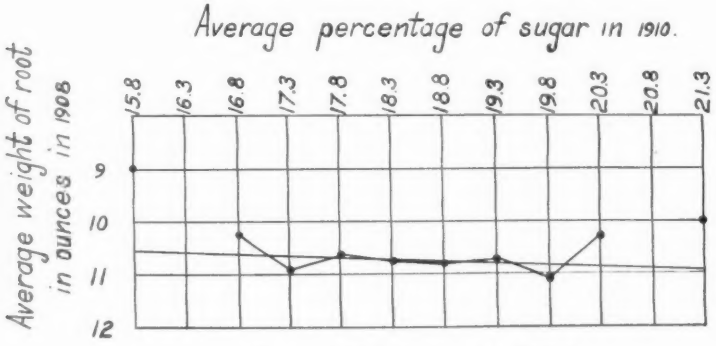

FIG. 35.—To accompany table XXXI

of the other pairs. The coefficients of correlation not only confirm this assumption but also have a corroborative effect upon one another.

Figs. 31–36 furnish a graphic illustration of the character of the material used and the reliability of the results. The trends of the empirical means of the separate classes represented by dots and connected by broken lines show a fairly close agreement with the straight line regressions. Moreover, there are no marked deviations of empirical means from the straight lines except where the classes are small. Hence the distributions are fairly regular and the biometrical constants are probably reliable.

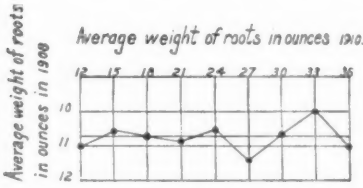

FIG. 36.—To accompany table XXXII

We are not justified in concluding from the foregoing results that no real differences in yield and quality occur, however, as real differences may be obscured by fluctuations. The most we

can say at present is that family differences of this character as determined by current field methods are not permanent.

DETERIORATION FROM LACK OF SELECTION.—There is a current belief that sugar-beets deteriorate in percentage of sugar when selection is discontinued, but this has not been proved satisfactorily. A gradual decrease for a limited period is not necessarily indicative of permanent reduction, as such environmental factors as sunshine, temperature, rainfall, time of planting, fertility of the soil, drainage, and cultural methods all vary in different years and these variations affect the percentage of sugar. In fact, the percentage may fall for 2 or 3 consecutive seasons and then rise again under more favorable conditions.

If sugar-beets deteriorate from lack of selection, commercial seed should produce poorer roots than seed of selected mothers, as it is grown from an intermediate steckling generation in which no selections are made. Such a comparison was made in 1913 by mixing seed of highly selected families of Morrison's Kleinwanzleben and planting it in alternate rows beside the commercial variety of the same stock. The results are shown in table XXXIII.

TABLE XXXIII

COMPARISON OF MORRISON'S COMMERCIAL SEED WITH SEED OF MORRISON'S SELECTED MOTHER BEETS

MORRISON'S SELECTED MOTHER-BEET SEED				MORRISON'S COMMERCIAL SEED			
Row number	Number of beets in row	Weight of row of beets in pounds	Percentage of sugar in beets	Row number	Number of beets in row	Weight of row of beets in pounds	Percentage of sugar in beets
2.....	68	46.5	15.0	3.....	67	43.5	15.9
4.....	68	37.0	15.0	5.....	65	32.5	15.2
6.....	60	39.5	15.2	7.....	62	37.0	15.4
8.....	72	40.0	15.1	9.....	70	39.5	15.5
10.....	62	38.0	15.2	11.....	72	43.0	15.3
12.....	82	47.0	14.9	13.....	69	36.5	15.7
14.....	85	49.5	15.0	15.....	57	33.0	15.7
16.....	74	45.0	14.9	0.....	0	0	0
Averages	71.4	42.8	15.0	.....	66	38.0	15.5

Average weight of root in grams: Morrison's commercial, 259.91; Morrison's selected, 271.70.

In every instance the commercial seed produced the richer roots. They were somewhat smaller than the roots from seed of selected mothers, averaging 11.79 gm. less per plant, but this is

equivalent to only about 0.03 per cent sugar, while the average difference obtained was 0.5. Hence the commercial seed not only failed to show deterioration, but actually appeared to improve. Similar results were observed between the variety and its more

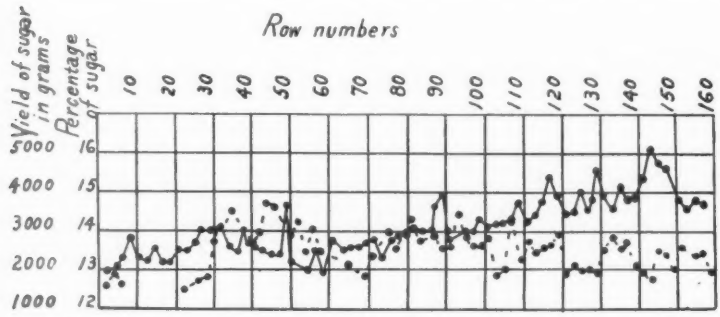

FIG. 37.—Effect of soil irregularities on relationship between percentage of sugar and yield of sugar in consecutive check rows, Madison, 1914; solid line indicates percentage of sugar; broken line, yield of sugar.

highly selected families in 1912 which led to the planning of this experiment.

RELATIONSHIPS BETWEEN PERCENTAGE OF SUGAR, YIELD OF SUGAR, AND AVERAGE ROOT WEIGHT OF SUGAR-BEET ROWS.—As

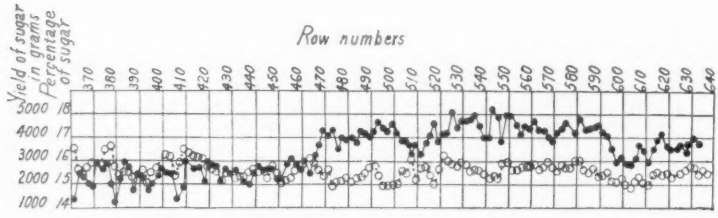

FIG. 38.—Effect of soil irregularities on relationship between percentage of sugar and yield of sugar in consecutive check rows, Madison, 1913; solid line indicates percentage of sugar; broken line, yield of sugar (corrected yield).

beets are grown under approximately uniform spacing, the same correlations which obtain between weight, percentage of sugar, and yield of sugar in individual roots would be expected to occur in sugar-beet rows. An ideal stand is never obtained under field

conditions, however, and as this may cause a deviation from the theoretical relationships, the actual relationships have been determined by plotting in figs. 37–50 the mean values of consecutive rows containing 80–100 per cent stand.

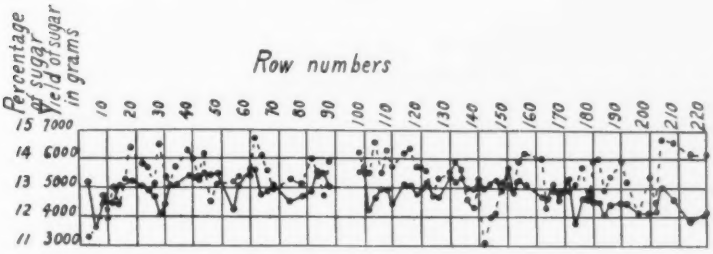

FIG. 39.—Effect of soil irregularities on relationship between percentage of sugar and yield of sugar in progeny rows, Madison, 1912; solid line indicates yield of sugar (corrected yield); broken line, percentage of sugar.

Figs. 37–41 show no correlation between percentage of sugar and yield of sugar in beet rows. In some places the graphs seem to follow a similar trend, as in rows 390–460 and 600–630 of fig. 38,

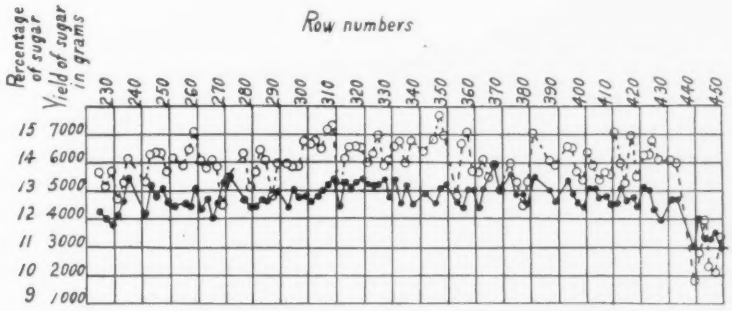

FIG. 40.—Effect of soil irregularities on relationship between percentage of sugar and yield of sugar in progeny rows, Madison, 1912; solid line indicates yield of sugar (corrected yield); broken line, percentage of sugar.

and 370–440 of fig. 40; but in other places, as in rows 100–160 of fig. 37 and 450–520 of fig. 41, they apparently diverge. On the average, therefore, percentage and yield vary independently.

A negative correlation occurs between percentage of sugar and average weight of root per row. The most marked occurrence of this kind is shown in the trends of figs. 44 and 45. Divergence is fully as evident, however, in more localized areas and even in

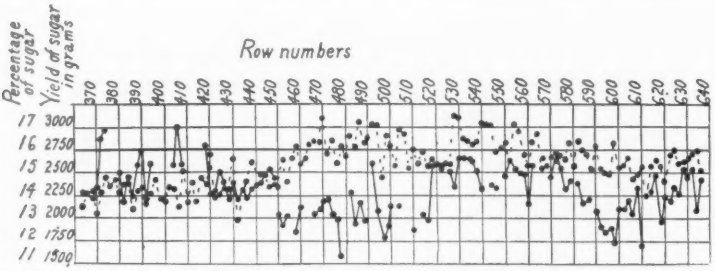

FIG. 41.—Effect of soil irregularities on relationship between percentage of sugar and yield of sugar in consecutive progeny rows, Madison, 1913; solid line indicates yield of sugar (corrected yield); broken line, percentage of sugar.

individual rows. Compare in this regard the divergence of graphs in rows 47, 72, 127, 157, and 162 of fig. 42, and 240–250, 255–265, and 370–380 of fig. 43.

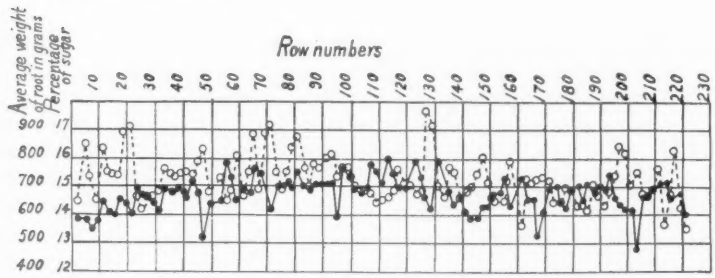

FIG. 42.—Effect of soil irregularities on relationship between percentage of sugar and average weight of root in consecutive check rows, Madison, 1912; solid line indicates percentage of sugar; broken line, average weight of root per row.

A high positive correlation is shown between average weight of root and yield of sugar per row in figs. 46–49. Whenever either graph progresses in a given direction, it is closely followed by the other member of the pair. This is most conspicuous in figs. 47 and 48.

As corrected yields, that is, yields corrected for a full stand by means of the regression coefficient between number of roots and yield of sugar per row, were employed in figs. 38–41, and actual yields in figs. 37 and 46–49, their relationship has been determined

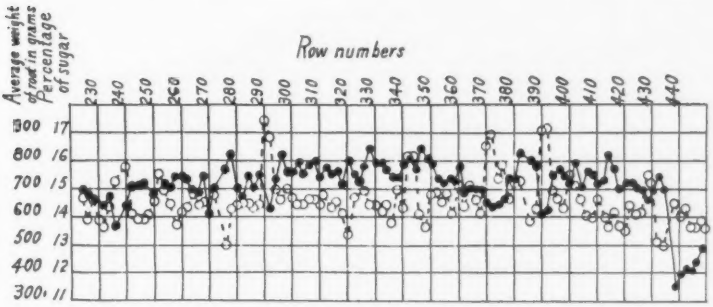

FIG. 43.—Effect of soil irregularities on relationship between percentage of sugar and average weight of root in consecutive check rows, Madison, 1912; solid line indicates percentage of sugar; broken line, average weight of root per row.

and illustrated in fig. 50. Only rows containing a stand of 80–100 per cent are connected. The *o*'s of the unconnected rows represent actual yields, and the *x*'s represent corrected yields of rows containing less than 80 per cent stand.

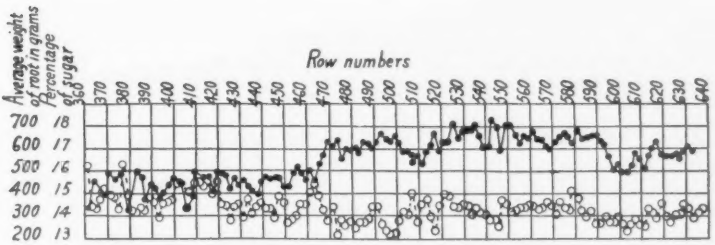

FIG. 44.—Effect of soil irregularities on relationship between percentage of sugar and average weight of root in consecutive check rows, Madison, 1913; solid line indicates percentage of sugar; broken line, average weight of root per row.

The graphs show practically the same progressions and trends. The use of actual yields instead of corrected yields, therefore, in some of the figures did not materially alter the results of comparison.

The relationships exhibited in the foregoing figures between yield and quality of beet rows have a very important bearing upon sugar-beet improvement. Selection for yield of sugar regardless

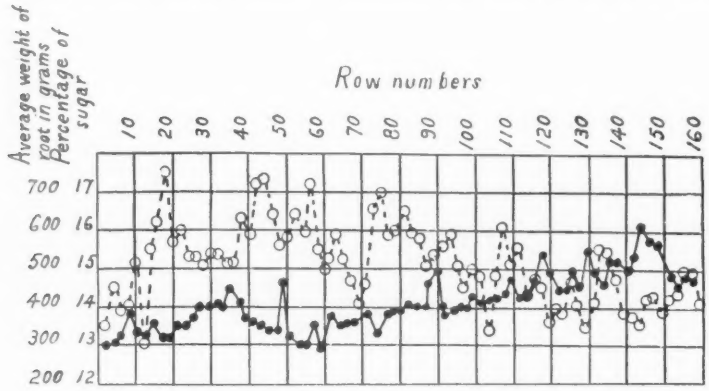

FIG. 45.—Effect of soil irregularities on relationship between percentage of sugar and average weight of root in consecutive check rows, Madison, 1914; solid line indicates percentage of sugar; broken line, average weight of root per row.

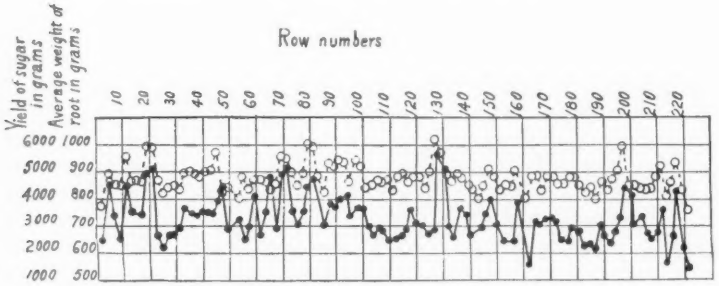

FIG. 46.—Effect of soil irregularities on relationship between average root weight and yield of sugar in consecutive check rows, Madison, 1912; solid line indicates average weight of root per row; broken line, yield of sugar.

of percentage would increase the size of the root but decrease the proportion of extractable sugar, as large roots have, not only a lower percentage of sugar than small roots, but also a lower coefficient of purity. On the other hand, selection for percentage alone would decrease the tonnage, as percentage of sugar is

negatively correlated with average weight of root. Both yield and percentage, therefore, should be considered in making selections. Obviously, the best single character is yield of extractable

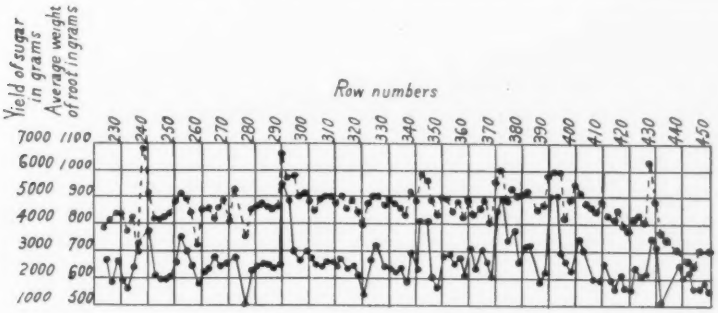

FIG. 47.—Effect of soil irregularities on relationship between average root weight and yield of sugar in consecutive check rows, Madison, 1912; solid line indicates average weight of root per row; broken line, yield of sugar.

sugar, but even with its use a lower limit should be set for percentage. The extra cost of determining coefficients of purity used in calculating extractable sugar, however, would probably condemn the use of this method for commercial purposes.

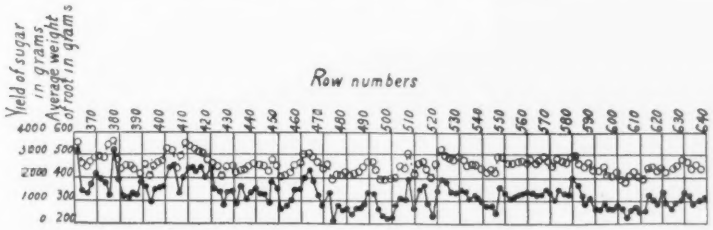

FIG. 48.—Effect of soil irregularities on relationship between average root weight and yield of sugar in consecutive check rows, Madison, 1913; solid line indicates average weight of root per row; broken line, yield of sugar.

Discussion of results

The results of the foregoing experiments may appear, at first sight, to disprove the possibilities of beet improvement, but this is only apparent. The fact of past improvement is beyond

question, as the average percentage of sugar, average size of root, and yield of sugar per acre have been increased greatly. Moreover, there is no valid reason for assuming that these characters have reached their maximum development. The differences exhibited by the varieties Morrison's Kleinwanzleben, Kleinwanzleben's Original, and Madison Original Selections, as illustrated in fig. 1, show that sugar-beet varieties may still be altered by breeding. For the sake of discussion it will be assumed that beets are improved

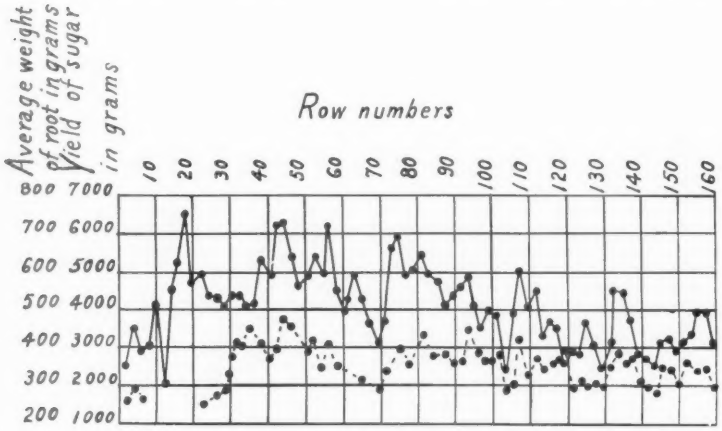

FIG. 49.—Effect of soil irregularities on relationship between average root weight and yield of sugar in consecutive check rows, Madison, 1914; solid line indicates average weight of root per row; broken line, yield of sugar.

either (1) by a gradual accumulation of small variations through the process of continuous selection, or (2) by the isolation and multiplication of an occasional mutation.

Continuous selection is based upon the theory that "like begets like," or the tendency of superior individuals to transmit their qualities to their progeny. As shown in the foregoing tables and graphs, the best roots transmit no better qualities than do mediocre roots. Their differences are mere fluctuations, therefore, and have no influence on beet improvement. This has no bearing, however, upon the value of continuous selection when applied to real differences, as the possibilities of improvement through a

gradual accumulation of small real differences is still an open question. Since aside from the progeny test no method of distinguishing real differences between beet roots has been in vogue, the selection of choice roots by chemical and physical means probably has played no part in sugar-beet improvement except where an occasional root has mutated and thus given rise to a superior physiological species.

The real differences between sugar-beet families are usually very small, as may be noted from the difference in size of corresponding

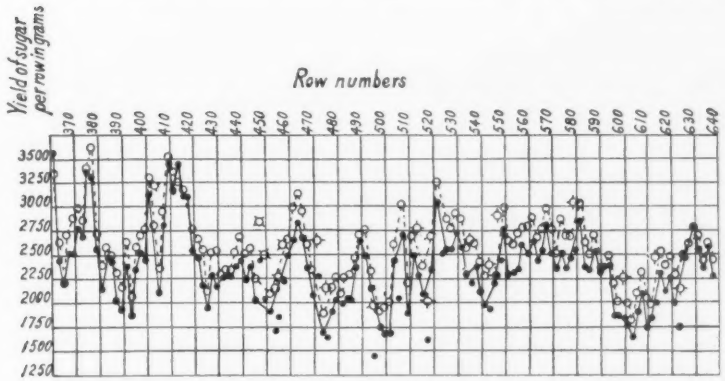

FIG. 50.—Relationship between actual yield and corrected yield of sugar in consecutive check rows, Madison, 1913; solid line indicates actual yield; broken line, corrected yield.

variations of individual check and progeny rows. In fact, their real differences are greatly exceeded by their fluctuations.

Both the best and the poorest families transmit average qualities. Hence continuous selection does not seem to be an efficient means of improvement. Moreover, it is difficult to conceive how it could have played any important part in sugar-beet improvement in the past.

The isolation of mutations probably offers more promising opportunities for improving beets than continuous selection. Our records show no evidence of mutations, but the numbers are too small to disprove their occasional occurrence. Moreover, no table presented contains data for more than two consecutive generations,

which is insufficient to determine with certainty either the fact or the frequency of their occurrence.

The mutations sought by the sugar-beet breeder are not necessarily morphologically distinguishable from other individuals of the variety. They are plants which have undergone constitutional alteration and hence possess new potential limits of physiological elasticity which they transmit to their progeny.

The valuable plants of this class are those which transmit a higher sugar-producing capacity to their progeny than possessed by the variety regardless of their own qualities. In fact, we are hardly justified in assuming that the mutants themselves possess conspicuously high qualities. They are more likely to lie near the mean of the variety than at either limit of its range. This is illustrated for a particular case in fig. 51.

The frequency polygon A shows the actual distribution of 3784 beets for percentage of sugar, while A^1 shows a similar distribution of the hypothetical progeny of a supposed mutant. Their means, represented by the vertical lines M and M^1, are 17.67 and 18.67 respectively, and hence differ by 1 per cent sugar. The bulk of the mutant's progeny in polygon A^1 lie between classes 17–21, which is about 22 times as great as the proportion lying above 21. Since the records of the progeny are an expression of the potentialities of the mutant, the mutant itself is 22 times as likely to lie between 17–21 in the original population of polygon A as above this group.

The possibilities of finding a mutant by taking a limited number of roots from the material represented in polygon A are somewhat greater in the classes above 21 than between 17–21. There are in polygon A about 100 times as many individuals in the classes 17–21 as above 21. If the mutant were equally likely to appear in either group, the chances of finding it by taking an equal number of roots from each group would be 0.01 as great in classes 17–21 as in the population above 21. However, we found that the chances of the mutant's lying in group 17–21 are 22 times as great as in the other group, therefore the possibilities of finding it by drawing an equal number of roots from each group are not as 0.01:1, but as 0.22:1, or about 1:4.5. If the whole polygon A were divided into two groups, so that all the roots containing 21 per cent sugar

or less were to lie in one group and all the remaining roots in the other, the chances of finding the mutant by taking an equal number of roots from the respective groups would be as 1:6.

The ratios 1:4.5 and 1:6 are small and hardly warrant the expenditure of large sums of money for chemically selecting

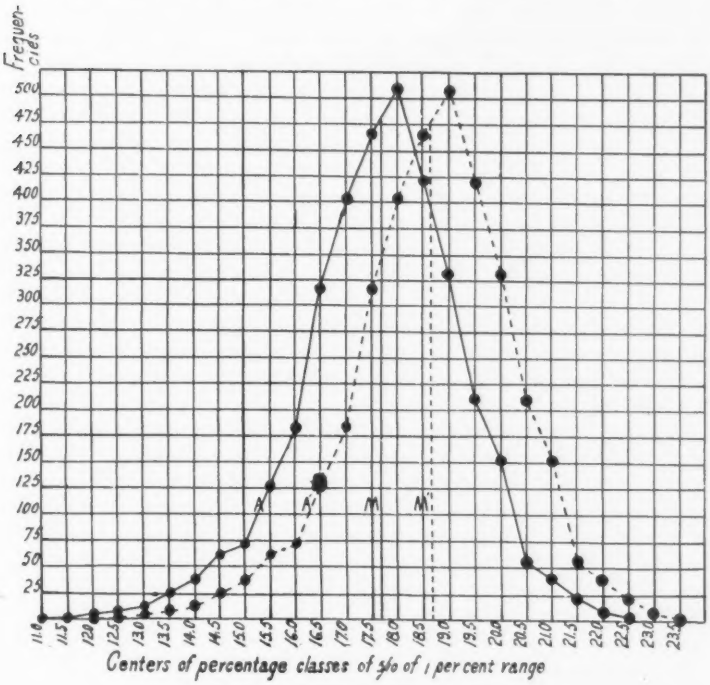

FIG. 51.—Most probable location of mutants

individual roots of high sugar content to increase the probability of finding mutants. Tests of 6–10 times the usual number of roots taken at random would be more economical and fully as effective.

As continuous selection has resulted in failure and only the mutation theory remains as a promising means of sugar-beet improvement, some very decided changes should be made in methods. First of all, more efficient methods of making tests should be devised in order to reduce the effects of soil irregularities

and distinguish real differences. This can best be accomplished by a more frequent use of checks and replications. Replications, however, require a liberal seed supply. Although a single plant ordinarily produces a limited quantity of seed, there are means of increasing the normal yield considerably. A root divided into halves and planted at the customary distances will produce nearly twice as much seed as a whole root. Moreover, seed yield is greatly influenced by soil fertility. A rich soil stimulates under a proper temperature the production of flowering shoots and enables the plant to mature a large crop. If these means are employed to increase the average seed production and only the heaviest seed-yielding plants are used for the preliminary tests, a sufficient quantity of seed may be obtained to make a large number of plantings from each individual. When a sufficient number of replications are made to distinguish real differences, only the few best families should be saved. As roots of a single family are apparently of equal breeding value, it is advisable to plant all the roots of each family in an isolated group, where distance or intervening obstructions will prevent their crossing with plants of a different family. There is apparently no gain from harvesting the plants of each family separately. Moreover, the combined yields of the individual plants of a family are necessary to make a satisfactory test of the relative merits of the families the following year. Thereafter, no further selection would appear to be necessary. If all but 3 or 4 of the best families are discarded and the remainder mixed and prevented from crossing with poorer stock, they probably will maintain their vigor and are not likely to deteriorate in the absence of further selection.

The possibility of further improvement apparently lies in the isolation of more valuable mutants, but whether the original stock or the new variety should be used as a source of material can be determined only when it is known in which the mutants will occur with the greater frequency.

SUMMARY OF BIOMETRICAL CONSTANTS COMPILED FROM TABLES II–XI, XIV–XXV, AND XXVII–XXXII

No. of table	Characters	Mean	Standard deviation	Coefficient of correlation
II	Percentage of sugar in root in 1905	19.23 ±0.042	0.977 ±0.029	
	Yield of seed per beet in ounces in 1906	8.94 ±0.179	4.199 ±0.126	−0.027 ±0.039
III	Percentage of sugar in root in 1906	20.77 ±0.065	1.296 ±0.046	
	Yield of seed per beet in ounces in 1907	11.87 ±0.267	5.357 ±0.189	0.074 ±0.050
IV	Percentage of sugar in root in 1908	23.60 ±0.056	1.021 ±0.039	
	Yield of seed per beet in ounces in 1909	9.68 ±0.305	5.547 ±0.216	−0.157 ±0.054
V	Percentage of sugar in root in 1909	20.18 ±0.052	1.63 ±0.036	
	Yield of seed per beet in ounces in 1910	3.94 ±0.139	4.36 ±0.099	0.098 ±0.032
VI	Percentage of sugar in root in 1910	18.72 ±0.031	1.16 ±0.022	
	Yield of seed per beet in grams in 1911	215.90 ±3.115	117.29 ±2.202	0.049 ±0.026
VII	Quantity of sugar per root in ounces in 1905	2.63 ±0.037	0.87 ±0.026	
	Yield of seed per beet in ounces in 1906	8.86 ±0.176	4.14 ±0.124	−0.082 ±0.026
VIII	Quantity of sugar per root in ounces in 1906	3.89 ±0.086	1.725 ±0.060	
	Yield of seed per beet in ounces in 1907	11.78 ±0.268	5.407 ±0.190	0.081 ±0.049
IX	Weight of root in ounces in 1905	13.94 ±0.202	4.748 ±0.143	
	Yield of seed per beet in ounces in 1906	8.94 ±0.179	4.200 ±0.126	−0.056 ±0.042
X	Weight of root in ounces in 1906	19.42 ±0.470	9.480 ±0.330	
	Yield of seed per beet in ounces in 1907	11.82 ±0.265	5.341 ±0.186	0.024 ±0.050
XI	Weight of root in ounces in 1910	18.96 ±0.151	5.78 ±0.106	
	Yield of seed per root in grams in 1911	216.75 ±3.086	118.44 ±2.182	0.071 ±0.026
XIV	Percentage of sugar in mother roots in 1908	20.53 ±0.032	0.472 ±0.023	
	Average percentage of sugar in progeny in 1910	13.60 ±0.068	0.998 ±0.048	−0.149 ±0.067
XV	Percentage of sugar in mother roots in 1912	16.31 ±0.081	1.065 ±0.058	
	Value of progeny rows for percentage of sugar in 1914 expressed in percentage of their checks	96.46 ±0.114	4.499 ±0.243	−0.040 ±0.076
XVI	Percentage of sugar in mother roots in 1912	16.31 ±0.081	1.065 ±0.058	
	Average percentage of sugar in progeny in 1914	13.61 ±0.074	0.972 ±0.052	−0.090 ±0.076
XVII	Ounces of sugar in mother root in 1908	2.44 ±0.029	0.53 ±0.021	
	Ounces of sugar per beet in progeny in 1910	3.70 ±0.038	0.68 ±0.027	0.032 ±0.050
XVIII	Ounces of sugar in mother root in 1906	3.28 ±0.107	1.21 ±0.076	
	Ounces of sugar per beet in progeny in 1908	2.43 ±0.032	0.36 ±0.023	−0.100 ±0.088
XIX	Ounces of sugar in mother root in 1907	4.67 ±0.063	1.413 ±0.044	
	Ounces of sugar per beet in progeny in 1909	4.01 ±0.040	0.897 ±0.028	0.104 ±0.044
XX	Weight of mother root in ounces in 1908	10.31 ±0.121	2.19 ±0.086	
	Ounces of sugar per root in progeny in 1910	3.74 ±0.041	0.75 ±0.029	0.092 ±0.055
XXI	Weight of mother root in ounces in 1906	16.22 ±0.548	6.19 ±0.388	
	Ounces of sugar per root in progeny in 1908	2.41 ±0.032	0.36 ±0.023	−0.115 ±0.087
XXII	Weight of mother root in ounces in 1906	16.22 ±0.548	6.19 ±0.387	
	Average percentage of sugar in progeny in 1908	21.73 ±0.074	0.84 ±0.053	0.168 ±0.086

SUMMARY OF BIOMETRICAL CONSTANTS COMPILED FROM TABLES II–XI, XIV–XXV, AND XXVII–XXXII—*Continued*

No. of table	Characters	Mean	Standard deviation	Coefficient of correlation
XXIII	Weight of mother root in ounces in 1908	10.29±0.121	2.19 ±0.086	
	Average percentage of sugar in progeny in 1910	18.50±0.047	0.84 ±0.033	0.055 ±0.054
XXIV	Weight of mother root in ounces in 1908	10.25±0.120	2.15 ±0.085	
	Average weight of progeny roots in ounces in 1910	20.61±0.242	4.33 ±0.171	0.023 ±0.056
XXV	Weight of mother root in ounces in 1906	15.74±0.565	6.33 ±0.400	
	Average weight of progeny roots in ounces in 1908	11.28±0.142	1.59 ±0.100	−0.095 ±0.089
XXVII	Average percentage of sugar in beet families in 1912	14.07±0.063	0.826±0.045	
	Average percentage of sugar in beet families in 1914	13.61±0.074	0.972±0.052	−0.229 ±0.072
XXVIII	Value of beet families for percentage of sugar in 1912 expressed in percentage of their checks	96.01±0.329	4.313±0.233	
	Value of beet families for percentage of sugar in 1914 expressed in percentage of their checks	96.35±0.330	4.315±0.233	0.089 ±0.076
XXIX	Ounces of sugar per root in beet families in 1908	2.33±0.014	0.24 ±0.010	
	Ounces of sugar per root in beet families in 1910	3.69±0.042	0.70 ±0.030	0.031 ±0.060
XXX	Average weight of root in ounces in beet families in 1906	18.8 ±0.391	4.30 ±0.277	
	Average percentage of sugar in beet families in 1908	21.7 ±0.077	0.85 ±0.055	0.056 ±0.091
XXXI	Average weight of root in ounces in beet families in 1908	10.75±0.070	1.15 ±0.049	
	Average percentage of sugar in beet families in 1910	18.52±0.054	0.89 ±0.038	0.054 ±0.060
XXXII	Average weight of root in ounces in beet families in 1908	10.74±0.067	1.139±0.047	
	Average weight of root in ounces in beet families in 1910	20.57±0.261	4.45 ±0.185	−0.0003±0.059

Summary

1. Differences in the size and sugar content of individual beet roots show no evidence of inheritance. They are fluctuations, therefore, and apparently play no part in beet improvement.

2. No correlation was discoverable between percentage or quantity of sugar in sugar-beet roots of ordinary sizes and their yield of seed, nor between their yield of seed and the average percentage of sugar in their progeny.

3. The fluctuations of beet families planted in progeny rows in alternation with check rows exceeded their real differences, but real differences were distinguishable by the use of a large number of replications (cf. fig. 1).

4. Areas of beets in an apparently uniform field of small dimensions showed a difference of 2 per cent sugar.

5. Percentage of sugar and yield of sugar of sugar-beet rows vary independently. Progeny rows should be graded on both percentage and yield of sugar, therefore, or on yield of extractable sugar.

6. The average weight of root per row increases with yield of sugar and decreases with percentage of sugar.

7. The discontinuance of selection for one generation caused no deterioration in percentage of sugar. In fact, there was some apparent gain.

8. No improvement in yield or percentage of sugar was obtained by continuous selection. Both the good and the poor families transmitted average qualities.

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POLLEN STERILITY IN RELATION TO THE GEOGRAPHICAL DISTRIBUTION OF SOME ONAGRACEAE[1]

CARL C. FORSAITH

(WITH PLATES XIX–XXI AND ONE FIGURE)

Before the development of methods of research in biology, the question of the origin of species was not debatable, since it was taken for granted that all had arisen as a result of special creation. LINNAEUS, however, in 1757 was convinced that this doctrine needed modification. His departure from the accepted hypothesis was brought about by the appearance of an intermediate form of *Tragopogon* resulting from a cross of *T. pratensis* and *T. porrifolius*, to which he gave the significant species name *T. hybridus*. Too much emphasis cannot be laid upon this fact, since it paved the way for the later and more complete conception of the fundamental laws of evolution.

From that time the occurrence of hybrid forms was recognized now and then, until the reality of their existence became universally admitted. During the later investigations of these plants, it became evident that hybridism was very closely correlated with that of a more or less sterile quality of the generative organs, in proof of which there has arisen a prodigious amount of literature. These numerous citations may well be considered as having established the general biological principle of sexual impotency resulting from earlier parental crosses. Since this form of degeneration is observed more readily in the microspores than in the megaspores, it naturally follows that the presence of a large and varying amount of infertile pollen may be considered as indicative of previous interbreeding of plants where such conditions obtain. Although this relation of pollen abortion to hybridism has become quite widely accepted, there appears to be still some doubt as to the validity of the general principle. Consequently, it may be advisable to mention a limited number of references in its support.

[1] Contributions from the laboratories of Plant Morphology of Harvard University No. 81.

In 1832 DUTROCHET (10) noticed the abortion of pollen grains in hybrids of *Prunus*. This relation, without doubt, received even greater recognition under DARWIN'S influence in 1859. The appearance of his *Origin of species* (5), in which he mentions the sterility of the offspring from hybrid parents, did much toward establishing this fact. The impaired fertility of garden varieties of plants likewise is valuable proof of this principle. The long-continued improvement of horticultural species by crossing has led to much investigation in this connection, and as a result many cases are on record where forms thus produced have become nearly or quite completely sterile. As an example of this form of sterility, conditions found in a garden hybrid of *Fuchsia* may be mentioned. This genus is well known to cross readily, and the resultant impotency of the sexual elements was observed by SMITH (22) in 1876. In his article he states that the pollen in garden fuchsias "is always variable." In a hybrid from *Fuchsia splendens*×*procumbens* he noticed that only about one-third of the pollen cells were triangular in form, and the remaining two-thirds were of a "peculiar shape" which (in view of our later studies) may be interpreted as an indication of a tendency to abortion in the anther. During the same year ANDERSON (1) states that only a few seeds in this species were potent, and a condition similar to this was cited by MEEHAN (21) in relation to cultivated varieties of *Viola* in 1889.

Since this article deals more especially with pollen conditions in the genus *Epilobium*, reference is made to HAUSSKNECHT'S (17) monograph of the genus, in which he mentions several hybrid forms. In his discussion of these crosses, he speaks of pollen sterility in relation to hybridization as follows: "Das beste Merkmal gewähren dann in diesem Falle die Pollenkörner, welche ich bei primären Bastarden in der kleinen und geschlossen bleibenden Anthere stets völlig verschrumpft vorfand. . . . ." Statements similar to this were made by GUIGNARD (16) two years later in regard to hybridization in *Cistus*, *Begonia*, *Mespilus*, and *Crataegus*, the pollen of which he describes thus: "Les grains de pollen fertiles représentent environs le quart du nombre total, le rest est formé de grains de dimensions moindres, presque vides de protoplasma, ou n'ayant qu'un noyau au moment de la maturité de l'anthère." In his later

discussion of a special case, he concludes as follows: "Ce resultat m'apparâit donc fournir un argument important en faveur de la nature hybride de la plante en question."

The advent of the mutation theory of DEVRIES added a new factor to this discussion, the results of which have appeared in numerous publications. A brief mention of a very few of these results in regard to the correlation of hybridization and sexual impotency will suffice. DEVRIES (**7**) speaks of reduced fertility in crosses of *Oenothera biennis*×*muricata* and *Cytisus laburnum*×*purpureus;* BEER (**4**) showed that all the pollen of *Oenothera longifolia* did not reach maturity, as there was not sufficient nutritive material to carry all the grains to completion; TISCHLER (**23**) described a *Bryonia* hybrid resulting from a cross of *Bryonia alba* and *B. dioica* thus: "Die Pollenkörner sind sehr haufig (bei GREGORY fast immer) degeneriert, und von sehr ungleicher Grösse"; and GATES (**12, 13, 14**) describes the cytological development in relation to pollen degeneracy in some hybrid species of *Oenothera*.

BATESON (**3**) has been very influential in establishing the principle of sterility as a result of hybridism. Numerous references to his own observations add much weight to the value of the probability that previous crossing is indicated by an important condition of the microspores. This proof is augmented likewise by many citations of the results obtained by other investigators of this phenomenon. Conclusions similar to these were obtained by JEFFREY (**18, 19, 20**) as a result of studies of a large number of the vascular cryptogams, conifers, and angiosperms. The results of his researches may be summarized briefly as follows. In the more constant and distinct species, the pollen grains are generally equal in size, full of protoplasm, and show no indications of an arrested development. On the other hand, those forms which show a large degree of fluctuation and contain known hybrids, generally present a varying amount of impotent pollen cells. These opposing conditions are strictly in accord with the general principle just mentioned. Consequently, JEFFREY was led to infer that those species which are characteristically constant and exhibit perfect pollen should be considered as pure. In contrast to this type of spore development, he regarded those forms which are habitually variable

and which present impotent microspores as hybrid segregates, or hybrid species.

In view of this great quantity of evidence in favor of the coexistence of hybridism and sterility, together with a habitual lack of contradictory proof, it seems safe to assume that these conditions illustrate a general biological correlation. Consequently, whenever there appears a large percentage of impotent pollen on the anther, the natural conclusion is that this sterile state has been brought about by previous ancestral crossing.

These facts naturally lead to the question of the stability of hybrids in nature, which the morphological evidence of pollen sterility reveals as such. This question can likewise be answered in the same manner as the first, namely, by reference to cited examples. BATESON (3) in his discussion of this subject mentions a number of instances where hybrids have remained constant, instead of following the usual Mendelian principle. In regard to this phenomena he states as follows: "Literature of hybridization and heredity abounds with examples of hybrids which are said to have bred true, or, as we should say, without segregation"; DE VRIES (7) in a similar discussion of *Oenothera biennis*×*muricata* mentions constant hybrids which resemble one parent more than the other; and DAVIS (6) in speaking of crosses of *Oenothera biennia* and *O. grandiflora* says that hybrids were produced which resembled *O. Lamarckiana* to such a degree as to justify the consideration as a working hypothesis that *O. Lamarckiana* arose as a hybrid, and (to quote more directly) "it will be apparent to the reader that if the evidence should finally indicate *Lamarckiana* to be of hybrid origin, as a number of writers have already suggested, many of the so-called mutants are likely to be interpreted as segregates splitting off according to Mendelian expectations." Thus it is apparent that there are numerous quite constant hybrids which may be considered as segregated species.

Having discussed the morphological indications of the relation of pollen sterility to that of hybridization, and the proof of the stability of hybrids thus formed, it is evident that these two so well established principles must have some bearing upon the origin of certain races of plants. At present there are two conceptions

in regard to the evolution of species. There is that of DARWIN (5) which states that new forms represent a gradual transition of the existing structure through a slow process of a natural selection of minor variations. In opposition to this doctrine, there is the DeVriesian hypothesis of mutation, which explains the origin of new forms by the sudden acquisition or loss of characters (known as germinal variations), which are inheritable and breed true to type. The strongest argument against this latter conception is presented by the fact that the so-called mutants, especially those of *Oenothera*, show all the morphological evidences of hybrid origin. Those who support this view of evolution, however, state that the sterility of the pollen is as much an evidence of mutation as hybridization, but they fail to show the distinct difference between so-called mutants and those forms which may represent segregates derived from hybrid ancestors.

The argument that there is no tangible evidence of a gradual evolution is always advanced as a refutation against the Darwinian doctrine. As BARTLETT (2) states, "the few who still hold that the selection of continuous variations would suffice to bring about specific differentiation can bring forward little or no evidence to support their view. The evidence all points to the utmost fixity of organisms, aside from mutations." This point of view is based upon an apparent lack of transitional forms which are, in fact, characteristically absent in so far as the exterior structure is concerned. This conception owes its origin to the paucity of fossil plants, and the highly altered state of the external features of the remains which have been preserved as carbonized or petrified material and impressions. On the other hand, the internal organization of the woody stem shows abundant evidence of a gradual transition, in striking contrast to a characteristic lack of proof of the sudden appearance and later utmost fixity of anatomical structures. Although the general principles of plant morphology, that is, retention, reversion, and recapitulation, have become firmly established, and although their value in solving evolutionary problems is widely recognized, it may be advisable to mention a few examples which will show their application to the doctrine of a slow and continuous development.

Studies in this direction have shown that there has been a gradual transition of the pitted tracheid from that form characteristically present in the lowest of the vascular cryptogams, to that type normally found in the higher plants. The vessel also shows evidences of a continuous and uninterrupted evolution from that form found in the Gnetales to the compositaceous type of conducting elements. In the case of the wood ray, all the evidence points to this type of development. In the lowest forms of the vascular plants the ray is represented by a slight transformation of the tracheary elements, which gradually give place to the uniseriate parenchymatous plate, characteristic of the conifers. In the Gnetales and the lower angiosperms, this modification of the fibrous material occurs as a band of intermingled ray parenchyma and lignified fibers (the aggregate ray). By a gradual transition of the included tracheids or libriform fibers to storage cells (the first stage of which is seen in the septate condition of the fibers) the broad compound ray is formed. The wood ray reaches its highest development in the more advanced angiosperms, where the aggregate form has become spread out into scattered plates known as diffuse rays. Similar evidences of a gradual transition are seen in the development and distribution of wood parenchyma. This proof of a slow and unbroken evolution of these several woody elements is based, not only upon a study of fossil and existent forms, but also upon a comparison of the relative relation of progressive and conservative regions of the plant.

The value of this evidence of a gradual transition of woody structures cannot be overestimated, since it represents facts supporting general principles and distinctive of all the vascular plants from the lowest to the highest orders. Consequently, any factors of so universal occurrence as the development of the woody stem, conditions as equally characteristic of ancient as of modern forms, cannot logically be considered as "little or no evidence" in favor of a dilatory and uninterrupted change to a different type of structure. Furthermore, when the amount of proof exhibited by a study of all the main groups of the higher plants is weighed against the quantitative examples of so-called mutations, its numerical predominance is strikingly in

favor of the Darwinian rather than the DeVriesian hypothesis of evolution.

In contrast to this slow transformation in plants, there are larger and more inconstant variations which are brought about as a result of hybridization. These differences, thus formed, may follow a strict Mendelian ratio, or become segregates which breed true to type. This manner of fluctuation is so well known, however, that any further discussion of it is manifestly unnecessary.

Turning again to the consideration of the probable origin of species by mutation, as advanced by those who are in favor of this view, it is at least significant that by far the greater majority of the so-called species thus produced have descended from ancestry whose genetical purity is questionable. The genus *Oenothera* has been mentioned so frequently in this connection that it naturally deserves special consideration. This genus has long been known to hybridize freely, and also to have produced constant generations from crosses as a result of a segregation of characters. To place so much weight upon such precarious evidence as a distinction between segregates and so-called mutants, therefore, appears from the morphological standpoint, at least, to be unjustifiable.

Since the question of mutation so intimately concerns the Onagraceae, it seems advisable to consider the probable occurrence of hybrids in a few genera other than *Oenothera*, as indicated by the morphological evidence of pollen sterility. In this connection the following species will be discussed in respect to the probable relation of pollen sterility to hybridism and geographical distribution, namely: *Epilobium angustifolium* L., *E. latifolium* L., and *E. Dodonaei* Vill. of the subgenus *Chamaenerion; Epilobium hirsutum* L., *E. luteum* Pursh, and *E. obcordatum* Gray of the section *Lysimachion; Clarkia pulchella* Pursh, *C. rhomboidea* Dougl., and *C. Xanthina* Gray; *Oenothera serrulata* Nutt.; *Gongylocarpus fruticulosus* Benth. and *G. rubicaulis* Cham. and Schl.; *Diplandra lepezioides* Hook. and Arn.; and *Zauschneria californica* Presl.

The material for investigation was selected from herbarium specimens, representing widely separated stations throughout the greater part of the ranges of these species. Mature buds were chosen and treated with alcohol and NaOH, which caused them to

swell to their original size. The pollen thus treated was examined microscopically, and the relative amount of abortive grains (those which were shrunken, small, or empty) was determined by a more or less careful count of several fields of view. The difference between the fertile and the sterile microspores is perfectly distinct. The fertile ones appear as fully developed uniform spores filled with protoplasm; while those which have become degenerate are small, shrunken, and empty. Those buds, however, which showed less than 5 per cent of infertile pollen were considered as representative of genetically pure descent. This figure was chosen by DORSEY (**9**) after a careful investigation of *Vitis*. In this genus species of unquestionable ancestry were shown by a careful count never to contain more than this ratio as a result of physiological conditions.

From this general discussion of the relation of pollen sterility and variation in respect to hybrid formation, attention may be turned profitably to a more detailed discussion of the *Chamaenerion* group of *Epilobium*. It is of interest to note that DEVRIES (**8**) has stated that the pollen in *Epilobium* is "wholly fertile," but the writer's observations have led to different conclusions in regard to microspore conditions in this genus. *Epilobium angustifolium* L., with few exceptions, presents good pollen grains in the anthers chosen from plants which were collected in the more southerly part of its range. This condition is significant, since this region represents that part of its zone where it is outside the influence of *E. latifolium* L. This uniformly pure condition of the male generative cells is, without doubt, due to the fact that in the more southern stations *E. angustifolium* is practically a monotypic species, owing to the absence of an ally with which it is able to cross. On the other hand, where the "great willow herb" grows within the range of *E. latifolium*, the pollen shows a tendency to abortion in a varying degree.

A still more comprehensive understanding of the apparent relation of pollen sterility to geographical distribution can be obtained by reference to figs. 1–8, text fig. 1, and list I. Fig. 1 shows the pollen of *E. angustifolium* L. as it appears in plants from Auburn, New Hampshire. It will be observed that all the grains

are of uniform size and full of protoplasm. Fig. 2, representing a much enlarged view of pollen from the same region, shows clearly that there are no defective grains, but that all are equally well developed. Fig. 3 illustrates similarly perfectly developed microspores from the anther of a "fireweed" collected near Pocono Plateau, Pennsylvania, and the uniform structure of the pollen

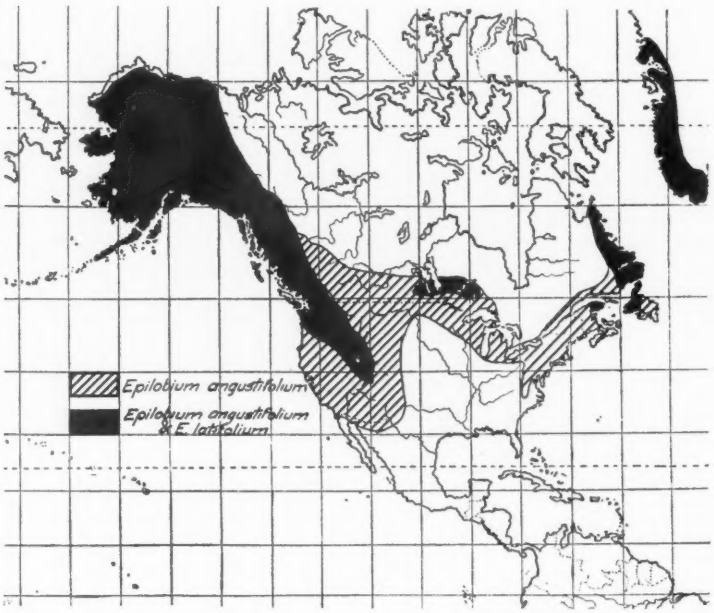

FIG. 1.—Relative distribution of *Epilobium angustifolium* L. and *E. latifolium* L.; solid black indicates region where the two species are coexistent; hatching indicates territory where *E. angustifolium* extends beyond range of *E. latifolium*.

from a West Virginia specimen is pictured in fig. 4. The two abortive grains among the perfectly formed ones in fig. 4, without doubt, have resulted from physiological conditions. In contrast to this perfect development of the pollen cells in these more southern representatives, fig. 5 represents the formation characteristic of the more northern regions where it grows within the range of *E. latifolium*. The pollen for this and the following illustration was chosen from a plant collected on Mount Albert in Gaspé

County, Quebec. Here, it will be observed, nearly one-third of the microspores are destitute of protoplasm, and all the grains, with a single exception, are much reduced in size. In fig. 6 similar indications of hybridism appear. In one case all the grains in a single tetrad, still remaining intact, have become defective. That like influences of degeneration may have caused many of the microspores of a Himalayan representative to stop growth in the early stages of development may be seen by reference to fig. 8. Several of the grains are perfectly developed, but a close observation will show also many small sterile pollen cells among those which have reached maturity.

A comparison of text fig. 1 and list I will show that there is a quite general tendency to abortion in that part of its range where *E. angustifolium* coincides with that of its nearest ally, *E. latifolium*. Defective microspores as an indication of hybridization are indicated by an asterisk in the list. In text fig. 1 those regions where these two plants are coexistent are represented in solid black. In contrast to this, those where *E. angustifolium* occurs alone are represented by hatching.

In view of the general principle of the correlation of pollen sterility and hybridism, previously mentioned, these facts are significant. From these studies it is apparent that when *E. angustifolium* grows within the range of its nearest ally, crosses take place which result in hybrid offspring. This relation is strikingly evident from the morphological standpoint at least, when one takes into account the presence of defective microspores in specimens chosen from that part of its habitat coterminous with that of *E. latifolium*. In contrast to this condition there is the more constant development of the pollen in buds selected from the more southern stations where *E. angustifolium* is practically monotypic.

LIST I

STATIONS OF *Epilobium angustifolium*, SHOWING RELATION OF PERFECT AND DEFECTIVE POLLEN TO LOCALITIES; DEFECTIVE POLLEN INDICATED BY AN ASTERISK

*Blanc Sablon River; Grand Falls, Newfoundland; East Avalon Peninsula, Newfoundland; *North of St. Paul's Bay, Cow Head, W. Newfoundland; *Curling, Bay of Islands, Newfoundland; *St. George's Pond, near Bay of

Islands, Newfoundland; Grindstone Island, Magdalen Islands, Quebec; *Seven Islands, Saguenay County, Quebec; *Lake Edward, Quebec; *Rivière du Loup, Timiscouata County, Quebec; *Mt. Albert, Gaspé County, Quebec; Table-topped Mountain, Gaspé County, Quebec; Little Métis, Quebec; Prince Edward Island; Kings Port, N.S.; Dead River, Somerset County, Me.; Fort Fairfield, Aroostook County, Me.; Jaffrey, N.H.; Mt. Washington, N.H.; Auburn, N.H. (figs. 1, 2); Mechanicsville, Vt.; Willoughby Notch, Vt.; Ashburnham, Mass.; Newton, Mass.; Southington, Conn.; Pocono Plateau, Pa. (fig. 3); Nescopec, Luzerne County, Pa.; Blister Swamp, Randolph County, W.Va. (fig. 4); *Mungo Park, Nipigon Lake, Ont.; *Brown County, Wis.; Keweenaw County, Mich.; Banff Clearing, Alberta, Can.; Center City, Minn.; New Mexico; *Bridge Park, Carbon County, Wyo.; *Artist's Glen, Colo.; *Weber River, Wahsatch Mountains, Utah; *Revelstocke, Selkirk, Can.; Carbonate Landing, B.C. (50° 30″ n. lat.); *Crane Lake, Assiniboia, Can.; *Emerald Lake, B.C.; Renfrew, Vancouver Island, Can.; *Silver City, Owyhee County, Idaho; Boise, Idaho; *Canyon County, Idaho; Clear Creek Canyon, Ormsby County, Nev.; Gunnerson Watershed, W. Cent. Colo.; Saturna Island, Humboldt Bay, Ore. Boundary; Clark Springs, Spokane, Wash.; Egbert Spring, Douglas County, Wash.; Swauk River, Kittitas County, Wash.; *Spalding, Ore.; Ten Sleep Lakes, Big Horn County, Wyo.; *Wahlamet, Douglas County, Ore.; Cold Water Canyon, San Bernardino County, Cal.; Waitesburg, Wash.; *Mt. Rainier, Wash.; Cascade Mountains (49° n. lat.); *Dutch Harbor, Unalaska, Aleutian Islands; *Makushin Bay, Unalaska; *Nazan Bay, Atka, Aleutian Islands; *Lake Lindman, Yukon River; *Disko, Greenland; *East Greenland; *Nain, Labrador coast; *Roma, Labrador coast; *Okak, Labrador; Hopedale, Labrador; Grand Lake, Newfoundland; *Newfoundland coast; *Table-topped Mountain, Quebec (fig. 7); *Mt. Albert, Gaspé County, Quebec (figs. 5, 6); *Turin, Marquette County, Mich.; Pagosa Springs, S. Colo.; San Francisco Mountains, Ariz.; Socorro County, N.M.; *Yellow Stone National Park; *Roger's Pass, Selkirk (51° 30″ n. lat.); Nagai Island, Schumagin, Alaska; Tulare County, Cal.; *Bighorn Mountain, Wyo.; *Nashes Fork, Albany County, Wyo.; *Yukon, Can.; Anvik, Alaska; *Pluma, S.D.; Paradisino, Italy; *Lucetheshend, Surrey, England; *Sapporo, Japan; *La Buillard, Vosges Mountains, France; Louette St. Pierre, Belgium; Hupeh Province, Central China; *Rimkin, Tibet (fig. 8); Manchuria; Kurrum Valley, Afghanistan; *Island in Okhotsk Sea, N. Pacific; *Quichjock, Lapland; Hakone, Japan; *Reykjahled, N. Iceland; *Deuthfoss, Iceland; Harx, Germany.

Epilobium latifolium L. shows a similar condition of pollen sterility as a result of past crossing of its progenitors. Out of 32 plants examined, only 4 were found to contain structurally perfect cells, in contrast to 28 which showed abnormally developed micro-

spores, ranging from 10 to nearly 100 per cent in some cases. It is not surprising that this species should show a larger degree of abortion than the allied member of the subgenus *Chamaenerion*, since its entire range coincides with that of *E. angustifolium* as represented by the solid black portion of text fig. 1. List II shows the relative amount of sterile and perfect specimens of pollen. Fig. 9 illustrates pollen conditions in *E. latifolium* L. collected in Newfoundland. Reference to this figure will show that nearly all of the grains (those which are small, empty, and shriveled) are degenerate. Fig. 10 pictures the microspore formation in a plant from La Plata Canyon in Colorado. It will be observed that all the grains, with a single exception, are shrunken, and the fully formed one is abnormal in having more than the usual number of germination pores. Evidences of hybridism in an Alaskan *E. latifolium* are indicated in fig. 11. In this illustration the infertile grains appear as shrunken cells which are destitute of protoplasm. It is of importance to note in this connection that there is a general tendency in *E. latifolium* to abortion, and this condition is still more suggestive when it is observed that this plant, throughout its entire range, is coexistent with *E. angustifolium*.

LIST II

STATIONS OF *Epilobium latifolium*, SHOWING RELATION OF PERFECT AND DEFECTIVE POLLEN TO LOCALITIES; DEFECTIVE POLLEN INDICATED BY AN ASTERISK

*Disko, Greenland; *Godthaab, Greenland; *Tessiastuk, Greenland; *Hamilton Inlet, Indian Harbor, Greenland; *Roma, Labrador coast; *Valley of Exploits River, Newfoundland; Bay of Islands, Newfoundland; *Rope Cove, Newfoundland (fig. 9); *Grand Cascapedia River, Quebec; *St. John River, Gaspé County, Quebec; *Dartmouth River, Gaspé County, Quebec; *La Plata Canyon, Colo. (fig. 10); *Gunnerson Watershed, W. Cent. Colo.; *Graymount, Colo.; *Clear Creek, Colo.; *Buffalo River, Wyo.; *Mary Baker Lake, Mont.; *Fort St. Michael, Alaska; *Mt. Rainier, Wash.; *Seattle Wash.; *Shunagan Feld, Alaska; Lake Indian, Upper Yukon; *Chugackik Bay, Alaska; *Yakutat Bay, Alaska (fig. 11); *Selkirk, 118° 20′ n. long. and 51° 45′ n. lat.; *Juneau, Alaska; *Cold Foot, Yukon River, Alaska; *Cape Nome, Alaska; *Nazan Bay, Atka, Aleutian Islands; Akutan, Aleutian Islands; Glacier River, Unalaska, Aleutian Islands; *Mountains of Colorado.

It has already been pointed out that those species in which hybridism is habitual generally show a well marked variation. In this connection it may be well to mention the genera *Rubus*, *Rosa*, and *Crataegus*, whose fluctuation is very pronounced, in proof of which the lack of agreement in regard to their classification among systematic botanists is significant. This type of variability likewise is very noticeable in a study of any large amount of herbarium material of *Epilobium*, such as was observed by the writer in his examination of specimens at the Gray Herbarium. It is equally important in this connection to state that HAUSSKNECHT (17) mentions 14 *formae* of *E. angustifolium*, 10 of *E. latifolum*, and 6 of *E. Dodonaei*. Thus it would appear that this subgenus presents capricious conditions of change similar to the genera just mentioned, which possess known hybrids and likewise present morphological evidences of pollen sterility as an indication of past interbreeding.

Epilobium Dodonaei Vill. is apparently subject to similar sterile conditions, since 2 out of the 3 specimens obtainable showed abortive pollen. This feature was also observed by Miss HOLDEN in Cambridge, England, as a result of an investigation of microspore conditions in relation to hybridism in this species and in *E. angustifolium* from Europe. The probability that crosses of this nature have taken place is strengthened by the fact that a hybrid from *E. Dodonaei*×*E. spicatum* is noted by HAUSSKNECHT as described by HENNIGER.

Before turning to other species of the Onagraceae it seems advisable to summarize briefly the behavior of the species already discussed. It is apparent that the section *Chamaenerion* presents features which are characteristic of genera subject to hybridization in nature, as indicated both by sterility of the pollen and by a well marked variation. It is also evident that there is a distinct relation between this morphological proof of intercrossing and the geographical distribution of the species. In those regions where *E. angustifolium* has an opportunity to cross with its close allies, the anatomical proof appears conclusive that such crosses have taken place. Evidences of this phenomenon are still further strengthened by the fact that whenever this plant occurs sufficiently far south for crosses with other species of the subgenus *Chamaene-*

rion to be impossible, its microspores are usually perfectly developed and there appears little indication of abortion.

Hybrids have long been recognized in the subgenus *Lysimachion*, of which many are mentioned by HAUSSKNECHT, the names and parentage of which can be learned by reference to his monograph of the genus. Since this subgenus contains so many species, extending over a wide and continuous territory, a study of the pollen conditions in connection with their geographical distribution is impossible. It is significant, nevertheless, that the 3 species examined (*Epilobium hirsutum* L., *E. luteum* Pursh, and *E. obcordatum* Gray) showed evidences of pollen sterility. Similar microspore conditions were observed by JEFFREY (19) in a hybrid derivative of *E. hirsutum*.

Since the pollen in all of these species remains in the tetrad formation, it furnishes an excellent example of the relation of abortion to the number of grains derived from the mother cell. In a recent discussion of this subject DEVRIES suggested that, since three of the megaspores in the angiosperms are sterile, we might be led to infer that all the higher plants are hybrids, "at least on the material side." It is evident, however, that this condition has no bearing upon the question, since this type of degeneration represents a constant feature, and one which is in no way affected by intercrossing. In contrast to this form of spore abortion, that mode normally exhibited by *Epilobium hirsutum* and *E. obcordatum* may be mentioned. In anthers which show no evidences of abortion, the 4 microspores in the tetrad develop equally, and all are full and fertile at maturity. Conditions analogous to these were found to obtain in *Zauschneria californica* Presl., as indicated in figs. 17 and 18. Those plants, nevertheless, which show indications of being segregates from hybrid ancestors, possessed degenerate pollen grains, but these defective spores bore no constant relation to the original number in the tetrad. Fig. 12 shows the pollen formation in an apparent hybrid derivative of *Epilobium obcordatum* Gray. The spores at the left of the figure are quite fully developed in respect to the number in the tetrad. A single exception appears in the lower of the two groups, where a single grain has failed to reach maturity. The remaining clusters, it will be observed,

present more evidences of deterioration, and a further study of the illustration will show also that a large and variable number of the microspores have failed to attain normal development. Thus it is apparent that the process of degeneration in hybrid forms is in no way related to the processes of abortion of megaspores in the mother cell. The evidently pure species of the subgenus *Lysimachion* and the monotypic *Zauschneria* present uniformly perfect development of all the spores in the tetrad. In anthers showing morphological proof of earlier contamination, however, the number of abortive grains is in no way related to the number of microspores in the mother cell, since all the 5 possibilities of degeneration obtain.

The pollen conditions in *Clarkia* are not especially different from those already described for *Epilobium*. Of 16 specimens of *Clarkia pulchella* Pursh which were examined, 8 were found to contain nearly uniformly potent pollen cells. The remaining 8, however, showed distinct evidences of hybridism, as revealed by a large percentage of infertile pollen. *Clarkia rhomboidea* Dougl. showed the results of degenerating influences in a far less degree, and only 1 of 10 buds investigated presented indications of sterility. *Clarkia Xanthina* Gray exhibited features similar to those already mentioned in the discussion of spore conditions in *C. pulchella*. One-half of the buds studied presented defective microspores. Fig. 13 shows the type of pollen presented by plants possessing no morphological evidences of spore degeneration. In contrast to this uniform pattern, however, fig. 14 pictures the spore conditions in plants which have apparently been derived from hybrid ancestors. It will be observed that about half of the grains are empty and shriveled, and are strikingly unlike the fertile cells illustrated in the figure. As the character of pollen sterility in *Clarkia* differs in one of the essential features relative to *Epilobium*, it will not be discussed at length. Furthermore, since the several species occupy the same region, it is but natural to assume that they are more or less inclined to intercross freely. The offspring from these unions, accordingly, show a large and varying amount of defective microspores. There is, on the other hand, a perfect development of the pollen where such crosses have not taken place.

A consideration of pollen conditions in a few of the Onagraceae would be far from complete without a brief mention of some species of *Oenothera*. For this reason the distinct *Oenothera serrulata* Nutt. was chosen. This form is considered by some to be sufficiently well defined to be regarded as a separate genus, *Meriolix*. Of 22 specimens which were examined in the usual way, all were found to contain more than 50 per cent of abortive pollen grains. The defective grains, as can be seen by reference to fig. 15, are strikingly distinct when contrasted with the few fertile microspores. Likewise, the great variability in this genus, as well as an abundance of natural hybrids, are so well known and so universally accepted, that any further discussion of these phenomena in relation to sterility in hybrids would be superfluous. It is significant, nevertheless, that this species should show so large a percentage of defective pollen, and, as such, presents a condition strictly in accord with the general principle previously mentioned.

In contrast to the degenerate pollen development in *Oenothera*, conditions in the anthers of *Gongylocarpus fruticulosus* Benth. and *G. rubricaulis* Cham. and Schl. should be mentioned. Both of these species show uniformly well developed microspores; there occur no indications of abortion in any of the grains. Similar spore formation was observed in *Diplandra lopezoides* Hook. and Arn., as illustrated in fig. 16. This shows all the cells to be equal in size and of uniform development. This naturally leads to the conclusion that the plants here mentioned have come from genetically pure ancestors. Although the genus *Gonyglocarpus* is considered by ENGLER and PRANTL (11) to be monotypic, 2 species were listed at the Gray Herbarium. The presence of two species, nevertheless, is unimportant from the standpoint of hybridism. *G. fruticulosus* is found in California, and *G. rubricaulis* grows near Vera Cruz, Mexico. The relative remoteness of these stations naturally precludes the impossibility of interfertilization, thus insuring in each a pure line of descent. The anatomical evidence of uncrossed species likewise supports this conclusion. All the pollen grains examined showed no indication of degeneration, but all were full of protoplasm and of equal magnitude.

Conditions of spore formation very similar to those described for the 2 species of *Gongylocarpus* were observed in *Zauschneria californica* Presl. It was possible to obtain only 4 specimens, but those presented microspore development such as might readily be expected in a monotypic genus. All the pollen cells were equal in size and fertility, as indicated by figs. 17 and 18. Fig. 17 represents a low magnification of the pollen of *Zauschneria*, and it will readily be observed that all the spores are perfectly developed. Fig. 18, a higher magnification, shows this fact even more conclusively. It is apparent also that all the spores in each tetrad reach maturity, and in no case do they show degeneration such as is habitual in 3 of the megaspores of the mother cell.

In respect to spore formation, this genus shows features parallel to those presented by the essentially monotypic *Gongylocarpus* and the geographically limited *Epilobium angustifolium*. The presence of entirely fertile pollen in these species is very significant. It is evident, of course, that hybridism is impossible. On this account all the specimens under consideration may be regarded as representative of pure lines of descent. That this purity of lineage is closely related to a perfect development of the pollen cells is strikingly evident from studies in this direction. The monotypic *Zauschneria* and the essentially monotypic species just cited generally present microspores which are perfect in every respect. Opposed to this type of spore formation, however, species possessing known or apparent hybrids generally contain pollen which is prone to abortion in varying degrees. Consequently, these 2 types of kindred phenomena show in a very conclusive manner the validity of the assumption that sterile pollen is reliable proof of hybrid lineage.

In the earlier paragraphs of this paper, the writer has attempted to show that there are certain general biological principles which have become firmly established. Naturally these principles have grown slowly, and have become far-reaching only in direct proportion to the amount of investigation carried on in relation to their application. Among the many laws thus formulated, that in regard to sexual impotency of hybrids is of the utmost importance in this discussion. The study of this problem, however, leads to

a consideration of the probable origin of species. As has already been stated, there are 2 distinct views in reference to this question. On the one hand, there is the idea of a gradual and continuous development; and on the other hand, the sudden and intermittent acquisition or loss of certain characters. These variations are said to breed true to type, and to form new and distinct species. The first of these conceptions receives very strong support from the characteristically gradual development of the woody elements in the lignified stem. These organs, as revealed by anatomical investigations, show a slow and continuous transition from the organization normally present in the lowest of the vascular cryptogams, to the form typical of the higher angiosperms. This support of the Darwinian hypothesis is still further strengthened by a characteristic lack of contradictory proof in the form of an intermittent course of development. Examples in favor of the opposing view represent isolated cases in certain groups of plants, of which the genus *Oenothera* has furnished the largest percentage. As has already been stated, there is a fundamental objection to the doctrine of mutation, especially in connection with *Oenothera*. This genus is well known to hybridize freely, and consequently the lineage of its so-called mutants must invariably be open to question.

This part of the discussion naturally leads into even narrower limits, that is, a recognition of hybrids in nature. In this connection there exists a general morphological proof of hybrid derivation. This condition is indicated by a distinct although variable percentage of abortive pollen grains in an anther. It should also be mentioned in this connection that most of the so-called mutants show this very evidence of hybrid descent.

It can readily be seen that the geographical distribution of a plant might have a direct influence on hybridization, and such has proved to be the case. *Epilobium*, especially the section *Chamaenerion*, furnishes an excellent example in this connection. *E. angustifolium* from those regions where it is essentially monotypic (the southern part of its range in the United States) presented generally perfect pollen. In contrast to this state, in specimens from the northern zone (where it is in contact with the allied

species *E. latifolium*) the pollen showed a strong tendency to abortion in varying degrees. Conditions similar to those were observed also in *E. latifolium*, and more generally in the subgenus *Lysimachion*, where there was quite habitual tendency to abortion of the microspores. This situation is due, without doubt, to the more constant presence of species between which crosses are possible.

In contrast to this condition, there is that presented by the 2 essentially monotypic species of *Gongylocarpus*, the geographically limited *Epilobium angustifolium*, and the strictly monotypic *Zauschneria californica*. In these plants there appears no evidence of pollen degeneracy, which (in view of the general principle of sterility in hybrids) is precisely the condition one would expect. It is, nevertheless, just as significant that these species which are unable to cross should present uniformly well developed pollen grains. This generally fertile state is in striking contrast to a habitual degenerate condition where there is frequent interfertilization. Thus it is apparent that reduced fecundity is valuable evidence of hybrid derivation, while a uniform development of the microspores is, other things being equal, as equally indicative of uncontaminated parentage.

From these studies of the Onagraceae in relation to geographical distribution, it is evident that impotent microspores are generally present in plants growing sufficiently near closely allied species to be the result of intercrossing. Opposed to this type of spore formation, there is a habitually perfect condition of the pollen chosen from plants growing in more isolated localities, and from monotypic species where interbreeding is manifestly impossible. Thus it is evident, from the morphological standpoint, that the Onagraceae intercross quite freely, and consequently there must be present many natural hybrids which greatly complicate genetical studies of species in this family.

Conclusions

1. It is apparent that abortive pollen, in a large though varying degree, is an indication of hybrid derivation.

2. There are many recognized hybrid segregates which have remained constant and true to type.

3. The relation of the geographical distribution in the subgenus *Chamaenerion* of *Epilobium* to hybridism is very pronounced. Whenever there is no possibility of intercrossing, the pollen is usually perfect. In contrast to this, there is a more general tendency to abortion in those regions where interbreeding is possible.

4. *Epilobium hirsutum*, *E. luteum*, *E. obcordatum*, and *Zauschneria californica* show conclusively that there is no relation between the number of microspores which may abort in apparent hybrid derivatives and the original number in the tetrad.

5. The essentially monotypic *Gongylocarpus*, the geographically limited *Epilobium angustifolium*, and the strictly monotypic *Zauschneria* present perfect pollen, a condition strikingly in accord with the general principle of hybrid sterility.

6. It is evident, on morphological grounds at least, that natural species crossing is a general feature among the Onagraceae, where such is possible in respect to geographical distribution and other factors.

In conclusion, the writer wishes to express his sincere thanks to Professors B. L. Robinson and M. L. Fernald for permission to obtain specimens from the Gray Herbarium; and to Miss Day, Librarian at the Gray Herbarium, for aid in securing literature. These investigations were carried on in the Laboratories of Plant Morphology of Harvard University, under the direction of Professor E. C. Jeffrey, and to him I am greatly indebted for advice.

Harvard University

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EXPLANATION OF PLATES XIX–XXI

FIG. 1.—*Epilobium angustifolium* L., showing entirely fertile pollen; ×75.

FIG. 2.—*E. angustifolium* L., showing perfectly developed pollen grains; ×125.

FIG. 3.—*E. angustifolium* L., showing no indication of abortion due to hybridism; ×150.

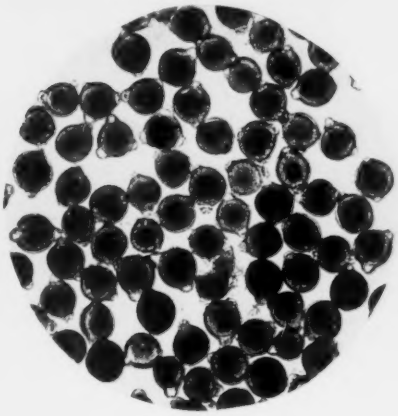
FIG. 4.—*E. angustifolium* L., showing fertile pollen; ×140.

FIG. 5.—*E. angustifolium* L., showing abortive pollen; ×125.

FIG. 6.—*E. angustifolium* L., showing fertile and abortive pollen, and a single tetrad in which all the grains are defective; ×125.

FIG. 7.—*E. angustifolium* L., showing indications of hybridism, as shown by the degenerate pollen grains; ×100.

FIG. 8.—*E. angustifolium* L., showing fertile and infertile microspores; ×200.



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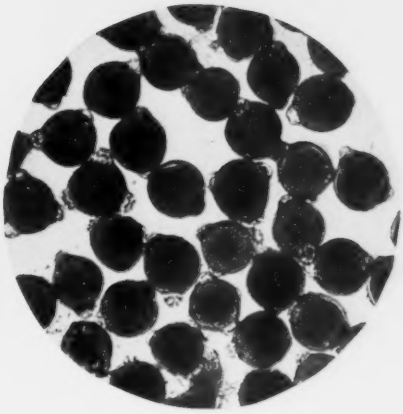

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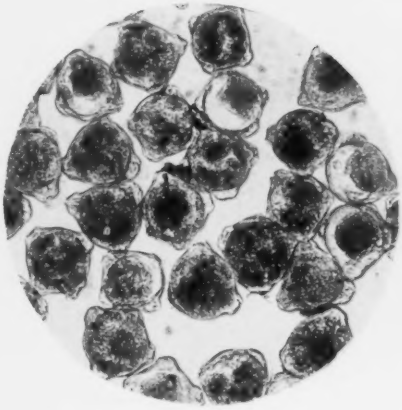

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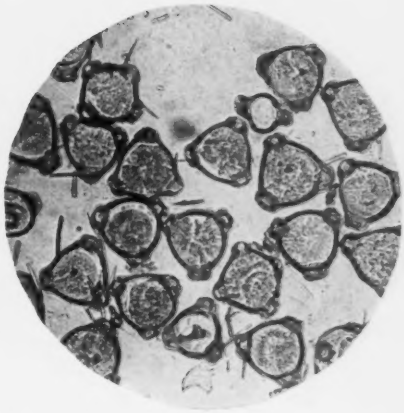

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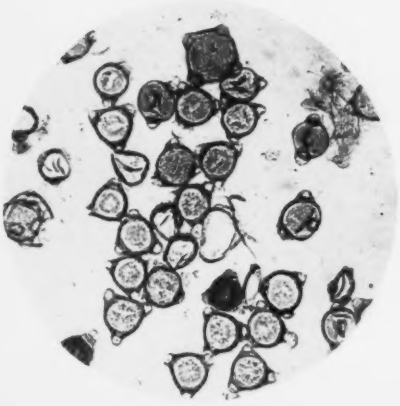

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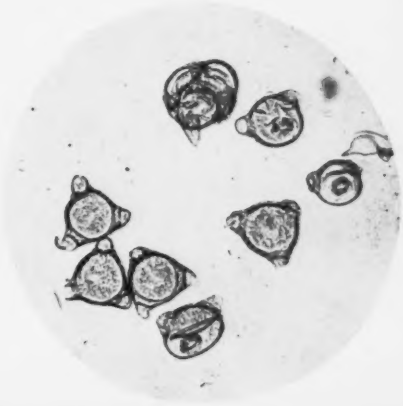

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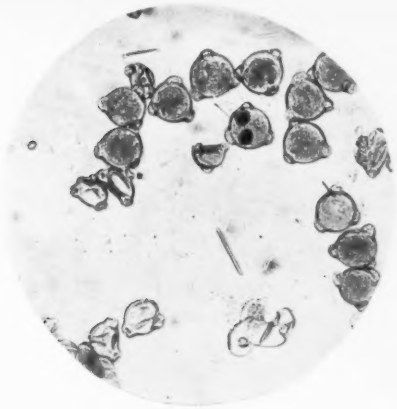
FORSAITH on POLLEN STERILITY



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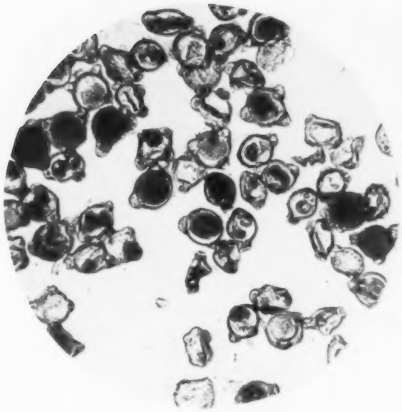

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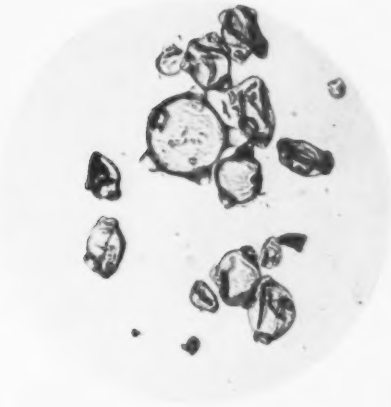

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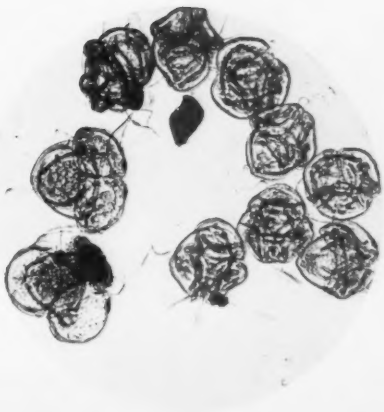

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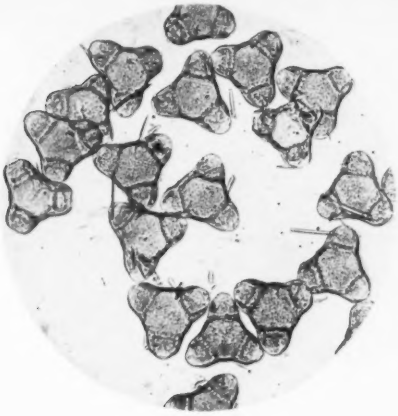

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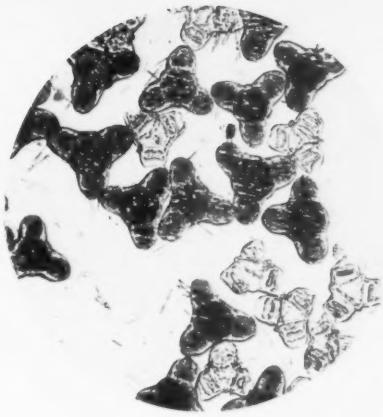

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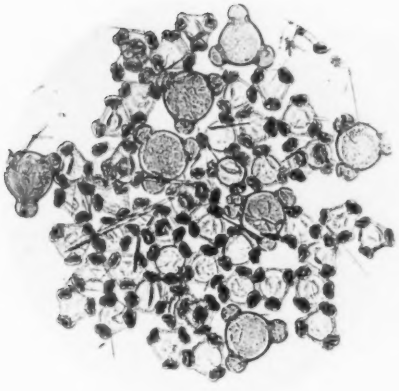

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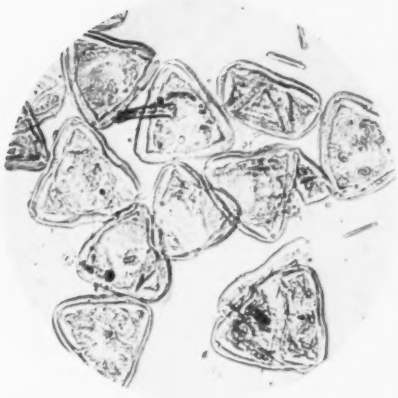

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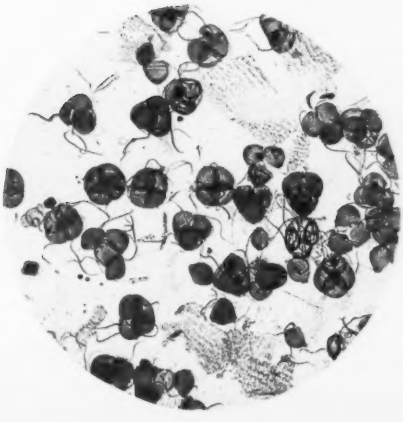

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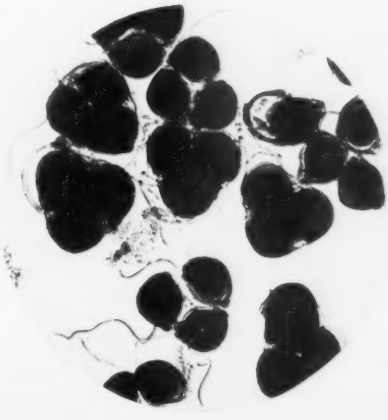

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FORSAITH on POLLEN STERILITY

FIG. 9.—*E. latifolium* L., showing evidences of abortion in a large percentage of the grains; ×75.

FIG. 10.—*E. latifolium* L., showing defective pollen; ×150.

FIG. 11.—*E. latifolium* L., showing perfect and imperfect pollen; ×125.

FIG. 12.—*E. obcordatum* Gray, showing fertile and abortive pollen grains in relation to tetrad; ×125.

FIG. 13.—*Clarkia Xanthina* Gray, showing uniformly developed pollen grains; ×125.

FIG. 14.—*C. Xanthina* Gray, showing fertile and infertile pollen; ×125.

FIG. 15.—*Oenothera serrulata* Nutt., showing relative size of fertile and degenerate pollen; ×125.

FIG. 16.—*Diplandra lopezoides* Hook. and Arn., showing functional microspores; ×200.

FIG. 17.—*Zauschneria californica* Presl., showing no indication of abortion in any of tetrads; ×50.

FIG. 18.—*Z. californica* Presl., showing tetrads in which all grains are uniformly developed; ×125.

THE EPIDERMAL CELLS OF ROOTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 221

EDITH ADELAIDE ROBERTS

(WITH SEVENTEEN FIGURES)

Introduction

The epidermal cells of roots have received more or less attention, especially those epidermal cells which form root hairs. The lines along which investigations have been conducted may be grouped readily under investigations made when the root is in an air medium and those made when the root is in a liquid medium. The factors in the air medium which have been discussed are moisture, light, temperature, contact, length of cells, mode of succession, position of nucleus, osmotic pressure, membranes, and food supply. The factors in the liquid medium discussed are calcium nitrate, potassium nitrate, salt, and bog conditions.

MOISTURE.—PERSECKE (**16**), working with *Zea mais* and *Pisum sativum*, states that the root hair development depends upon the amount of air and water in the interstices of the soil. SCHWARZ (**20**), using the same forms, comes to the conclusion that there is a minimum of moisture at which the hair formation begins, an optimum in which the best development is obtained, and a maximum where the hair development nearly or entirely ceases. PFEFFER (**18**) and others attribute more importance to moisture than to light as a factor in hair development. The conclusion from these observations is that moisture is a factor in the determination of the formation or non-formation of an epidermal cell of a root into an outgrowth called a root hair, but how or why this is so receives no consideration, nor do the limits of the amount of moisture necessary to become a limiting factor.

LIGHT.—The effect of light upon cells in general was investigated by KRAUS (**14**), who found that darkness increased the length of cells. DEVAUX (**2**) found the same and that this favored

the development of root hairs on corn. On the other hand, EWART (5), in the formation of root hairs on the root tendrils of *Vanilla*, found darkness accelerating and light retarding their formation. In this work, however, the moisture factor was not eliminated. PETHYBRIDGE (17) found that light retarded the formation of hairs upon oat and corn roots grown in water cultures. SCHWARZ (20) found that light and darkness had no effect on the root hair formation. SNOW (21) states that the effect of light and darkness, if any, is indirect. Light, then, as a factor has been experimented with to some extent with varying results, possibly owing to the fact that it has been associated with other factors.

TEMPERATURE.—No work on temperature as a single factor has been carried on. SCHWARZ (20) found that a temperature of 27–28°C. did not overcome the inhibitory effect of water as the roots grew smooth. SNOW (21), working with high temperatures plus moisture, found a decreased hair production brought about by the increasing elongation of the internal cells.

CONTACT.—The effect of contact has received some attention. SCHWARZ (20) observed that water roots upon entering the substratum develop hairs, and that when the soil is saturated the hairs on corn seedlings disappear, although soil particles are still present, and suggests that it may be due to chemical stimuli or retardation of growth, since it could not be due to contact. PFEFFER (18) denies that contact is a factor, for he found that on climbing roots hairs were produced on the side near the support where there is the greater moisture. SNOW (21) grew corn seedlings between plates and found no hairs on the sides touching the plates, while there were hairs on the other two sides; but again moisture may be the limiting factor and not contact.

JUEL (11) associated short cells and root hairs, as also did VAN TIEGHEM (25) and KRAEMER (13), and he finds that short cells remain short if they do not form root hairs. LEAVITT (15) finds two types of potential root hair cells. The first is that in which any cell of the outer layer may acquire the character of a root hair (trichome) by putting out a hair. This is characteristic of the dicotyledons, of some divisions of the monocotyledons, and of the Filicales. The second type is that in which they originate as

specialized elements. These cells differ in the formation of their cell plate, the wall lies somewhat diagonally, and the cell differs from the other epidermal cells in shape, size, and content. This type he finds in the Schizaeaceae, *Equisetum*, *Azolla*, *Lycopodium*, *Phylloglossum*, *Isoetes*, *Selaginella*, and in Nymphaeaceae. SNOW (21) finds that no definite length can be given as the limit for the formation for hair development; that in some roots the average length of piliferous cells is less than that of the smooth cells, but that the differential elongation of the epidermal and cortical cells is important, and that hair formation depends upon their ratio, that is, between the capacity of the epidermal cells to elongate and their ability to do so.

BARDELL (1) comes to the same conclusion as SNOW. A few of the measurements given by BARDELL are shown in table I.

TABLE I

Plant	Length cortical cell (mm.)	Haired epidermal cell (mm.)	Hairless epidermal cell (mm.)
Pisum sativum.....	231	161 (−71)	191 (−40)
" "	179	139 (−40)	172 (− 7)
Zea mais.....	69	66 (− 3)	77 (+ 8)
" "	69	69=	77 (+ 8)
" "	40	55 (+15)	55 (+15)
" "	36	0	33 (3)
" "	124	58	62

It is difficult to draw the conclusion which is given, for in the one case a difference of 40 mm. in length between epidermal and cortical cells calls forth a root hair; while in another the same difference accounts for the absence of a root hair, and measurements equal to, or greater than, or less than, seem to account for haired or unhaired epidermal cells.

SUCCESSION.—SCHWARZ (20) found that hairs were always produced in acropetal succession, while DEVAUX (2) asserted that new hairs could appear among the old ones; whereas HABERLANDT (8) agrees with SCHWARZ (20), emphasizing the fact that no new hairs ever arise among existing ones.

POSITION OF THE NUCLEUS.—HABERLANDT (8) noted the position of the nucleus in *Brassica alba* to be at the tip. In *Pisum*

sativum he finds that the protrusion of the root hair takes place opposite the nucleus. KÜSTER (**12**) takes exception to this. In the figures in SNOW'S (**21**) work the nucleus has no definite position.

OSMOTIC PRESSURE.—PFEFFER (**18**) found the osmotic pressure in corn root hairs to be greater than that of the cortical cells. STIEHR (**23**) found that root hairs on seedlings of *Spergula* which had grown in moist air when put in a 1 per cent magnesium solution burst at once, the nucleus being thrown out, and that always a greater percentage of the younger hairs burst. GANONG (**7**) found that the root hairs of *Salicornia* withstood 90 per cent salt water, *Suaeda maritima* 60–70 per cent, and *Atriplex patulum* 40 per cent. DRABBLE and LAKE (**3**) found that in mesophyll cells in plants growing in the same condition the osmotic pressure of the cell sap is generally the same, and in the plants of any area the osmotic pressure varies with the physiological scarcity of water. FITTING (**6**), using cells from the leaf, found that species showing high pressures in dry desert conditions show much lower pressures in moist situations, and concluded that certain plants adjust their osmotic pressure to the medium. ECKERSON (**4**) found that the root hairs were plasmolyzed by sucrose, varying from 0.20 μ to 0.30 μ. STANGE (**22**) found that in water cultures with nutrient solutions of high concentrations the osmotic pressures of roots are much higher than others; bean and pea in moist soil have pressures of 6.25N KNO_3 when growing in concentrated medium.

MEMBRANES.—SCHWARZ (**20**) found that the membrane of the root hair of *Taxus baccata* was of two parts: an inner layer which stains blue with chlorzinc iodide, and an outer layer which stains yellow brown. This outer layer is a mucilage which is hard in dry soil, and as moisture increases strongly swells and finally goes into solution. The mucilage layer gives no color with iodine and sulphuric acid, but stains red in an alcoholic solution of acid carmine. HESSE (**9**) measured the thickness of the membranes of the root hairs of many plants. He found that the thickness varied greatly with the family, but is nearly uniform within the family; that in any plant the thickness of any root hair mem-

brane varies with the medium; and that in *Rosa canina* growing in a dry situation the root hair has a stiff pointed apex and that the membrane is of lignin, but that in moist air no lignin is found.

LIQUID MEDIUM.—*Calcium nitrate.*—SCHWARZ (**20**) found that 15 per cent of calcium nitrate inhibited hair production. KRAUS (**14**) found roots richly haired in calcium nitrate.

Potassium nitrate—BARDELL (**1**) found that the root hairs on *Zea mais*, *Triticum vulgare*, *Avena sativa*, and *Tradescantia* sp. tend to decrease as the fractional solutions of KNO_3 increase in strength from 0.01 normal to 0.09.

Salt.—HILL (**10**) found that in *Salicornia* and *Suaeda* the root hairs can regulate their osmotic pressure in proportion to the osmotic pressure of the soil water.

Bogs.—TRANSEAU (**24**), working on bog plants, found that *Larix* roots when not surrounded by water develop root hairs abundantly. RIGG (**19**) used the development of the root hairs of *Tradescantia* as an indicator of the presence of toxins.

FOOD SUPPLY.—SCHWARZ (**20**) found that in reducing the food supply by removing portions of the endosperm the length of zone of root hairs decreased. SNOW (**21**) experimented with *Helianthus* and found that those with the most cotyledon remaining had the best formation of root hairs.

Investigation

This investigation was prompted by the fact that the presence or absence of root hairs is so often used as an indicator of the effect of changed external conditions. That the effect of the varying conditions might be known, it seemed well to try to determine the varying factors within the epidermal cell of the root, as well as the effect of the varying factors without and their reciprocal relations.

In order to picture as definitely as possible all the forces which might be affecting the epidermal cell, we may consider the average epidermal cell as having the form similar to fig. 1. Here it is seen that on four sides (*2*, *3*, *4*, *5*) the epidermal cell adjoins another epidermal cell, while on the inner side (*6*) it faces the wall

of a cortical cell, and on side *1* it is exposed directly to the varying external conditions.

In fig. 2, which is a median section of fig. 1, the following factors need to be considered: (1) *air medium*, (*a*) the physical character of walls *1*, *2*, *4*, *6*; (*b*) the chemical nature of walls *1*, *2*, *4*, *6*; (*c*) the osmotic pressure on both sides of walls *2*, *4*, *6*, and inside *1*; (2) *liquid medium*, (*a*) the physical character of walls *1*, *2*, *4*, *6*; (*b*) the chemical nature of walls *1*, *2*, *4*, *6*; (*c*) the osmotic pressure on both sides of walls *1*, *2*, *4*, *6*; (3) *length of cells*.

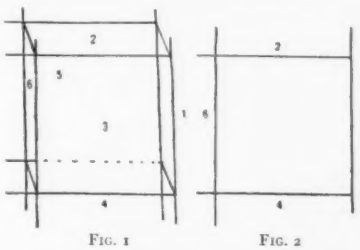

FIG. 1 FIG. 2

FIGS. 1, 2.—Fig. 1, form of an epidermal cell; fig. 2, median section of fig. 1.

A few measurements were made of the length of walls of cortical cells in comparison with the length of adjoining haired and unhaired epidermal cells. These were taken upon the same corn

TABLE II

Condition	Epidermal cell in mm.	Adjoining cortical cell in mm.
Haired	35	30
"	45	30
"	37	37
"	60	50
"	44	40
"	37	55
"	40	50
"	20	10
"	40	40
"	60	60
Unhaired	40	80
"	45–40	80
"	40	40
"	20	20
"	12	20
"	32	42

root, the haired epidermal cells being those just above water and the unhaired just below water, with the results shown in table II. These measurements, although few, indicate that there is no

definite relation between the length of the cortical cell and the epidermal cell which decides whether the epidermal cell shall become extended into an outgrowth or not. Fig. 3 shows a haired cell longer than the adjoining cortical cell, and fig. 4 shows two short epidermal cells adjoining one cortical cell. These measurements are corroborated by observations made throughout the work, many forms and all possible variation in length of cortical and epidermal cells being found.

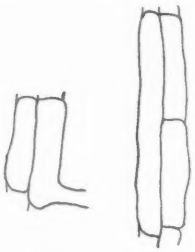

FIG. 3 FIG. 4

FIGS. 3, 4.—Fig. 3, haired cell longer than adjoining cortical cell; fig. 4, two short epidermal cells adjoining one cortical cell.

Position of nucleus.—The position of the nucleus has been found to have no relation whatever to the hair or to its initial formation. When the wall first swells, the entire wall bulges; later there is a greater swelling in one portion of it, the nucleus may not be near that portion; if the nucleus is near that portion, it may not follow the growth of the hair and be found near the tip of the hair, but remain in the base of the hair or in another part of the cell. There appears to be no relation between the position of the nucleus and the formation of the hair.

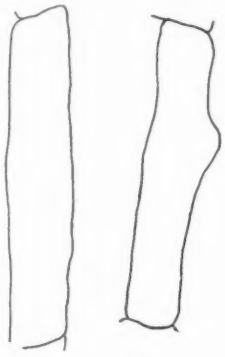

FIG. 5 FIG. 6

FIGS. 5, 6.—Fig. 5, bulging of entire wall; fig. 6, showing a narrowing of the swollen portion.

1. IN AIR MEDIUM

a) *The physical character of walls 1, 2, 4, 6.*—The first evidence of the formation of a root hair is the bulging of the entire wall *1*, as shown in fig. 5; then a portion of the wall stretches more than the rest and there is a narrowing of the swollen portion, as in fig. 6; but it may be noted that the base of a root hair is always greater in diameter than the rest of the hair, as in fig. 7. Seedlings of endive and lettuce demonstrate this fact. Branching of the hairs is common, indicating a difference in the physical character of the

wall *1*. Sometimes the branch will be of less diameter than the main hair, as in fig. 8; and again branches will be of equal diameter, as shown in fig. 9.

The stretched condition of the wall is evidenced by the fact that in some root hairs which are grown in moist air the membranes burst when the hairs are placed in water, or in a solution which has an osmotic pressure lower than that of the root hair cell, as shown in fig. 10; whereas plasmolysis occurs when the root hairs are placed in a solution of higher osmotic strength (fig. 11). The root hair remains normal when placed in a solution of an osmotic pressure equal to that of the cell content, as in fig. 12.

FIG. 7.—Base of the root hair greater in diameter than the rest of the hair.

FIG. 8 FIG. 9

FIGS. 8, 9.—Fig. 8, branch of the root hair of less diameter than the main hair; fig. 9, branches of equal diameter.

FIG. 10

FIG. 11

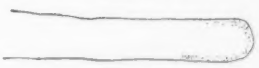

FIG. 12

FIGS. 10–12.—Fig. 10, root hair grown in moist air and placed in water, membrane burst and content escaped; fig. 11, root hair which has been in a solution of an osmotic pressure higher than that of the root hair; fig. 12, root hair placed in a solution of an osmotic pressure equal to that of the cell content.

The following forms when grown in moist air and then mounted in distilled water were found to burst immediately: alfalfa, barley, cabbage, mustard, *Nasturtium*, radish, *Xanthium*, and wheat. These when mounted in a solution of sucrose of an osmotic pressure equal to the osmotic pressure of the cell in question remain unbroken, whereas plasmolysis occurs if a solution of higher osmotic pressure is used. The cells burst at the tip and a part of the content of the cell is ejected. The nucleus is thrown

out if it happens to be at the tip of the root hair, but in case it is in or near the base of the cell it remains within the root hair. The break in the wall is immediately closed as the membrane springs back, and it is hard to detect the point of rupture except for the position of the escaped protoplasmic contents. The younger cells are more likely to burst than are the older ones. Fig. 13 (*a*) shows a radish root hair mounted in 0.24M sucrose solution; fig. 14 (*b*) is the same cell after being put in a 0.40M sucrose solution. It is to be noted that the walls corresponding to *2*, *4*, *6* are only very slightly changed, and wall *1* has decreased, thus showing that even in the same cell the physical condition of wall *1* is unlike that of walls *2*, *3*, *6*. In cells which do not burst when mounted in water, the surface of wall *1* is increased, as evidenced by a swollen tip which may or may not assume odd shapes. This indicates that wall *1* of these plants has a greater resistance, thereby indicating a variation in the epidermal cells of different plants, as well as a difference in wall *1* from walls *2*, *4*, *6*.

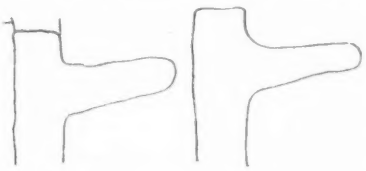

FIG. 13 FIG. 14

FIGS. 13, 14.—Fig. 13, root hair mounted in 0.24M sucrose; fig. 14, root hair after being placed in 0.40M sucrose.

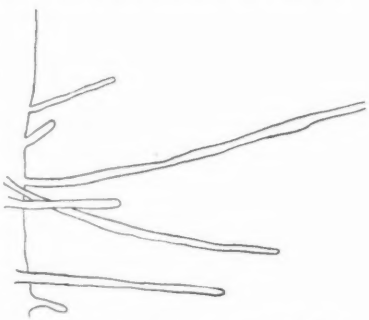

FIG. 15.—Short root hairs mingled with long ones.

It is frequently seen in many forms, for example, alfalfa, cabbage, and *Verbascum*, that short root hairs are mingled with long ones, giving the appearance of younger and older ones being together (fig. 15). The difference may be one of time of formation or of a variability in the growth of wall *1;* at least in these forms the length of the hairs is not a grading one as seen in the forms usually figured.

b) The chemical nature of walls 1, 2, 4, 6.—It will be seen from table III that a majority of the forms investigated have a wall made up of two parts, an inner membrane which gives the cellulose reaction with 75 per cent H_2SO_4 and IKI, and an outer membrane which stains red with Ruthenium red, denoting pectin. That this membrane is calcium pectate is shown by the fact that on the addition of ammonium oxalate the membrane breaks down and calcium oxalate crystals are formed. It will be seen that some forms have a third membrane at the tip of the root hair. This membrane stains with all the callose stains, blue with aniline blue and resorsin blue, red with corallin soda. It will be noted that corn is the only form examined which has one membrane and that of cellulose.

TABLE III

Plant	Chemical nature of root hair membranes		
	Inner	Outer	At tip
Alfalfa	Thin cellulose	Thick pectin	
Amaranthus	" "	" "	
Barley	" "	" "	
Corn	Thick "	.....	
Corn salad	Thin "	Thick "	Callose
Cabbage	" "	Thin "	
Daucus carota	" "	" "	
Morning-glory	" "	" "	
Mustard	" "	" "	Callose
Nasturtium	Thick "	Thick "	
Pea	" "	" "	Callose
Sisymbrium	Thin "	Thin "	
Tobacco	" "	Thick "	
Tradescantia	Thick "	Thin "	Callose
Vanilla	Thin "	" "	
Ceraptopteris	Thick "	" "	Callose

The walls *2*, *4*, *6*, and *1* are alike in that they all have an inner membrane of cellulose and an outer membrane of calcium pectate, but differ in that the calcium pectate membrane on wall *1* is thicker, and in some instances in the presence of callose at the tip of the hair. The calcium pectate membrane on side *1* is continuous with the middle lamella of calcium pectate of walls *2*, *4*, *6*. There is then a secretion of calcium pectate about the entire cell.

The relative thickness of the membranes having cellulose and pectin layers varies with the different plants, the cellulose layer being uniform over the hair, while the pectin is quite often thinner near the tip. Fig. 16 shows the tip of the root hair of *Nasturtium* with the two layers, the outer of pectin, and the inner of cellulose. Fig. 17 shows another *Nasturtium* root hair after it had been in ammonium oxalate; the calcium pectate has been changed to calcium oxalate and pectic acid. The calcium oxalate crystals are shown in the figure. The addition of Ruthenium red now gives no color except a faint tinge of pink about the crystals, due to the presence of pectic acid. Within the cell there are always masses of pectic substances; this is not calcium pectate, as it does not break down on the addition of ammonium oxalate, but still gives the color with Ruthenium red after treatment with ammonium oxalate.

FIG. 16 FIG. 17

FIGS. 16, 17.—Two layers of the root hair membrane; fig. 17, *Nasturtium* root hair after being in ammonium oxalate.

Either of the membranes may be removed by treating the cell with their respective solvents. The calcium pectate membrane is soluble in 2 per cent HCl and 2 per cent KOH, the cellulose is soluble in copper-oxide-ammonia.

The fact that the soil particles are held to the hair by the transformation of the outer layer into mucilage has long been accepted, but what that mucilage is has not been known. In the case of corn growing in the soil or in quartz sand, the mucilage was found to be of cellulose, whereas in a *Coleus* root growing in the soil the soil particles are held to the hair by a pectin mucilage.

It has been known that the epidermal portion of the seedling from which hairs arise stains brown when put in a 2 per cent solution of potassium permanganate, and that the region just above that of the hairs is not colored by the solution. This has often been used to differentiate in a general way the stem and root regions of a seedling. The chemical nature of these walls was determined. The external wall of the epidermal cells above those forming root

hairs has without the calcium pectate membrane on side *1* of the epidermal cell a third thin layer which is of cutin. It stains red with Sudan III and is insoluble in 50 per cent chromic acid. This wall *1* of the epidermal cell of the stem is then chemically different and physically of greater rigidity.

c) The osmotic pressure on both sides of walls 2, 4, 6, and on inside of wall 1.—The cortical cell is always plasmolyzed by a solution of sucrose which is 0.02M–0.04M stronger than that which plasmolyzes the epidermal cell; this indicates that on the outside of the wall *6* there is a greater pressure than on the inside; whereas on the outside of *2* and *4* there is a pressure equal to that on the inside. On the outside of wall *1* there is a pressure of one atmosphere. The variation between the outside and inside pressures of wall *6* is small, but there is a great variation in the pressures upon the two sides of wall *1*. Table IV gives the osmotic pressure of the root hairs of different plants grown under similar conditions.

TABLE IV

Plant	Osmotic pressure of root hair	Plant	Osmotic pressure of root hair
Alfalfa	0.24M sucrose	Lettuce	0.30M "
Amaranthus	0.30M "	Mustard	0.22M "
Barley	0.40M "	Nasturtium	0.28M "
Corn	0.28M "	Pea	0.22M "
Corn salad	0.28M "	Radish	0.28M "
Cabbage	0.28M "	Sisymbrium	0.24M "
Celery	0.30M "	Sunflower	0.22M "
Daucus carota	0.24M "	Turnip	0.30M "
Endive	0.24M "		

It will be noted in table IV that all are plasmolyzed by a solution of sucrose between 0.22M–0.30M sucrose, except barley. This is the equivalent of 5.10–7.70 atmospheres. Two facts are indicated here: first, that in moist air there is a minimum of difference of 4 atmospheres between the pressure upon the inside and upon the outside of wall *1;* and second, that under similar conditions there is a remarkably slight variation in the osmotic pressure of root hairs of seedlings of different genera. Some roots respond more readily than others to the percentages of moisture present in the media. Cabbage, alfalfa, squash, and corn show a definite

response. The formation of the root hair is inhibited by removing the covers of the Petri dishes in which the seedlings are growing. Regions of no root hairs, corresponding to the growth made during the removal of the cover, followed in regions of hair formation at the period of its replacement.

A series of corn seedlings was grown in air of a known moisture content. This was controlled by percentage solutions of sulphuric acid. The corn was soaked for 24 hours and then hung on cork plates in bottles which were one-third filled with the varying solutions. The bottles, which were corked and paraffined, were all placed in a water bath kept at 24°C. The measurements in table V represent in each case the average of 5 sets.

TABLE V

Solution	Length of root in cm.	Diameter of root in mm.	Length of hair in mm.
Water	3.0	70	80
1 per cent H_2SO_4	1.0	64	70
2 " " "	2.0	65	70
3 " " "	3.0	63	66
4 " " "	2.0	60	50
5 " " "	1.5	70	70
6 " " "	1.5	60	50
7 " " "	1.5	55	50
8 " " "	1.0	65	60
9 " " "	1.5	66	41
10 " " "	1.0	64	23
11 " " "	1.0	61	24
12 " " "	1.0	70	10
13 " " "	1.0	70	10

Table V shows that the cutting down of the moisture content affects the length of the root hair more than the length of the root or the diameter.

2. IN LIQUID MEDIUM

a) *The physical character of the walls.*—There is a variation in the wall of the corn in different media. In moist air the wall is uniform; in water when formed the hair is thickened at the tip.

b) *The chemical nature of the walls.*—The chemical study of the walls is under investigation.

c) *The osmotic pressure on both sides of 1, 2, 4, 6.*—The only wall on which the osmotic pressure may be made to vary at will is on the outside of wall *1*. Radish seedlings were grown in sucrose solutions of increasing concentrations in order to vary the osmotic pressure on the outer wall. The results obtained as the average of several series are given in table VI.

TABLE VI

Grown in	Diameter root in 1/100 mm.	Length hair in 1/100 mm.	Osmotic pressure	Difference between osmotic pressure of root hair and medium
Air	60	.....	28	28
Water	40	50	38	38
0.02 molecular sucrose	40	30	42	40
0.04 " "	40	20	42	38
0.06 " "	40	40	42	36
0.08 " "	40	50	49	32
0.10 " "	20	20	40	30
0.12 " "	40	60	42	30
0.14 " "	55	60	44	30
0.16 " "	30	40	48	32
0.18 " "	0	10	0	0
0.20 " "	0	20	0	0
0.22 " "	20	10	50	38
0.24 " "	30	10	65	41
0.26 " "	30	20	60	34
0.28 " "	50	20	65	37
0.30 " "	40	40	65	35
0.32 " "	30	10	0	0
0.34 " "	40	40	70	36
0.36 " "	15	10	75	39
0.38 " "	20	10	65	27
0.40 " "	30	20	0	0
0.42 " "	20	15	0	0
0.44 " "	50	15	70	36
0.48 " "	70	15	75	29
0.48 " "	0	0	0	0
0.52 " "	50	20	80	28
0.60 " "	50	0	90	30
0.65 " "	50	10	100	35

It is seen that as the concentration of the media increases the osmotic pressure of the root hair increases almost in direct proportion. Thus the root hair maintains an osmotic pressure from 4 to 6 atmospheres above that of the medium.

Differential media.—The effect of different media on the two sides of a seedling root was determined. Petri dishes were filled with the solutions, seeds were attached to the edge, and the roots

grew upon the solutions. The upper half of the root was in moist air and the lower half in the solutions. The roots grew straight, so that curvature could not account for the difference in the formation of the root hairs.

TABLE VII

Plant	Diameter of root in mm.	Length of hair (in mm.)	
		In air	In solution
Helianthus.....	8	8	1 (0.25M sucrose)
"	8	5	1 (0.20M "
"	5	5	1 (0.10M "
"	5	5	1 (0.05M "
Radish.....	5	8	2 (0.10M "

Discussion

The measurement of the length of cell walls as an indication of differential growth seems of little value unless the number of the cells in any region is taken into account. Since there is not an epidermal cell corresponding to each individual cortical cell, it would seem that the sum total of the epidermal cells should be known in order to determine differential elongation as a factor. So far as known, the measurements taken were of individual adjoining cortical and epidermal cells.

BARDELL'S own measurements show that for corresponding epidermal and cortical cells there is no definite relation in length which would cause the epidermal cell to produce a root hair, as neither do the measurements found here on corn.

The factors which determine the initial swelling of the outer wall of the epidermal cell are of primary importance, while other factors come in which determine the later growth into a root hair.

It has been proved in root hairs that there are portions of wall *1* less resistant than others. The bursting of the root hair, the swelling, the branching, and the varying thickness of the membrane, all give evidence of this. The indications are that such weaker places exist in the membrane at the time of root hair formation, although this has not yet been proved definitely. These weaker regions would determine the region of the wall in which the locali-

zation of swelling takes place, which immediately follows the initial swelling of wall *1*.

The position of the nucleus can have nothing to do with the initial swelling, as the swelling is over the entire length of the wall *1*. Since the weaker places bear no relation to the position of the nucleus, the nuclear position can in no way affect the formation of the root hair.

In this discussion the second type given by LEAVITT is not considered, the type in which only specialized epidermal cells form root hairs. Preliminary observations indicate that the osmotic pressure of the short cells varies from that of the other cells, but there are doubtless other factors determining the hair formation.

Investigations so far indicate that there are two factors of importance in the initial formation of root hairs. One is the unequal pressure acting upon either side of wall *1;* the other is the variation in the physical character of the wall.

The difference in pressures on the two sides of walls *2*, *4*, *6* is so much less than the difference on the two sides of wall *1* that it is negligible. The osmotic pressure of the root hairs of the plants investigated when grown in moist air shows slight variation. In the plants examined the osmotic pressure approximates 5 atmospheres. The walls *2*, *4*, *6* have an opposing pressure equal to or greater than 5 atmospheres, but wall *1* must sustain a pressure of 4 atmospheres, for on this wall the internal pressure is opposed by only one atmosphere, when the root is grown in moist air. This pressure is sufficient to account for the initial swelling of wall *1*.

The result of increasing the osmotic pressure on the outside of wall *1* by growing radish seedlings in sucrose solutions of increasing osmotic value proved that the opposing pressures on either side of wall *1* still maintained a balance of at least 4 atmospheres in favor of an outward pressure.

Root hair formation is retarded when the moisture content of the air is decreased. This is shown by the experiments with seedlings grown in Petri dishes in alternating dry and moist air, and in those grown over sulphuric acid solutions. Reduced moisture affects the membranes by decreasing the extensibility of the walls due to an increase in the elasticity of the colloids. The osmotic

pressure of the cell content is also increased by the modification of the moisture content of the air, but this is less effective because of the greater effect of the reduced moisture content upon the character of the wall.

The effect of reduced moisture content is again demonstrated in the experiments with differential media. In the case of *Helianthus* the effect of the sucrose molecule upon the colloids of the membrane and in the radish of glucose is to decrease the moisture content and the extensibility of the wall.

The wall is found to be composed of an outer membrane of calcium pectate and an inner membrane of cellulose. The only exception so far is in corn. A partial third membrane of callose is present in some. The amount of callose is so small and so little is known of its chemical nature that for the present it seems unimportant. The cellulose layer is important in that it gives greater strength to the wall.

The pectin layer and also the pectic substances within the cell are very important in the absorption and the retention of water, since pectin is a hydrophyllous colloid; and for this reason must influence the development of root hairs. The cations and the anions of the mineral substances in solution increase or decrease the absorptive capacity of this membrane according to a definite known manner, as indicated in the lyotropic series, investigations upon which should be made.

Summary

1. The initial formation of the root hair is indicated by a general swelling of the outer wall of the epidermal cell.

2. The swelling is produced if the physical resistance of the wall is overbalanced by the higher osmotic pressure which is maintained on the inside of the wall.

3. Further swelling followed by growth takes place at the less resistant portion of the wall.

4. This region bears no relation to the position of the nucleus.

5. The wall of the root hair is composed of two parts, an inner membrane of cellulose and an outer membrane of calcium pectate.

6. The presence of this membrane, together with the fact that the soil particles are held to it by a pectin mucilage, accounts for the high efficiency of the root hair as an absorbing organ.

UNIVERSITY OF CHICAGO

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BRIEFER ARTICLES

OCTAVE LIGNIER

(WITH PORTRAIT)

The subject of this sketch was born at Pangy in Champagne in 1855, and died at the comparatively early age of 61. His studies were carried on at Lille, under BERTRAND, GIARD, and GOSSELET. He received the doctorate later at Paris, but the environment of Lille seems to have exercised a greater influence on his subsequent scientific work. Lacking personal fortune, his life was a perpetual struggle to improve the small initial equipment he found at Caën, where he was made professor in 1887. His scientific achievement, in spite of this handicap, was more notable in the 25 years of his professorial activities (celebrated in January 1913) than usually distinguishes capacity favored by fortune and environment. More than 200 articles emanated from LIGNIER'S laboratories, and his activities covered the important fields of general morphology, anatomy, paleobotany, and plant geography. This wide range of interest was due partially to the fact that at first he had to cover the entire field of botany (including even a large herbarium), for only in later years was it possible to relegate certain curatorial and instructional duties to others. More decisive than necessity in the wide scope of his scientific activities were his untiring energy, capacity, and optimism.

Notable among his paleobotanical studies are those on Cycadofilicales, Bennettitales, Coniferales, etc. In the first group he described an interesting new genus *Mittagia* (resembling *Lagenostoma*), characterized by megasporangia not solitary but in sori, and also by the presence of 4 functional megaspores in each megasporangium.

The author's studies on the fossil floras of Normandy are of importance. In dealing with fossil conifers he did not make the mistake of certain German and English anatomists, in regarding rays as of paramount diagnostic significance. A supposed palm leaf *Propalmophyllum liasanum*, described by our author from the Lias, is according to ZEILLER of very problematical value. From the same geological level LIGNIER described remains of Cordaitales and Calamodendreae, a much later occurrence of these ancient types than has hitherto been recorded.

Important anatomical results reached by the author independently of, but in conformity with, workers on this side of the Atlantic were the conclusion that the herbaceous is derived from the woody type of stem, and that leaves are of great importance in the evolutionary history of plants. He divided vascular plants on the basis of the morphology of the leaf into Phylloideae and Phyllineae. The Phylloideae represent the Lycopsida, with the Equisetales and Sphenophyllales left out. The Phyllineae correspond to the Pteropsida, with the Equisetales and Sphenophyllales added (under the caption of Articulatae). SCOTT has further added to the latter the Psilotaceae and erected them into the phylum Sphenopsida.

LIGNIER'S activities were so numerous and important that it is impossible to do justice to them here. Botanical evolution has suffered a great loss in his death.—E. C. JEFFREY, *Harvard University*.

CURRENT LITERATURE

NOTES FOR STUDENTS

Current taxonomic literature.—B. BALFOUR and W. W. SMITH (Notes Roy. Bot. Gard. Edin. **9**:63, 64. *pl. 148.* 1915) describe and illustrate a new genus (*Beesia*) of the Ranunculaceae from northern Burma and Yunnan, China. —R. BENOIST (Not. Syst. **3**:176–180. 1915) has published 6 new species of *Qualea* and *Lecythis* from South America.—E. P. BICKNELL (Bull. Torr. Bot. Club **42**:549–570. 1915) in the 16th article on the "Ferns and flowering plants of Nantucket" enumerates the Compositae and describes a new golden-rod (*Solidago aestivalis*).—S. F. BLAKE (Jour. Bot. **53**:56–58, 103–104, 135–137, 153–158, 193–202, 225–235, 306–307, 322–324. 1915) has published a "Revision of *Salmea* and allied genera," describes new speceis in *Amaranthus, Heterosperma, Notoptera, Otopappus, Perymenium, Verbesina,* and *Zexmenia* from Mexico, Central and South America, and includes also a new genus (*Steiractinia*) of the Compositae to which 6 species are referred, all being indigenous to northern South America. The same author (Kew Bull. 348. 1915) has published a new genus (*Stenocarpha*) of the Compositae from Mexico.—F. BÖDEKER (Monats. für Kakteenkunde **25**:76–80. 1915) describes and illustrates a new species of *Mamillaria* (*M. multihamata*) from Mexico.—A. BRAND (Rep. Sp. Nov. **14**:146–156. 1915) under the title "Neue Borraginaceen Studien" describes several new species and raises the section *Mattiastrum* Boissier of *Paracaryum* to generic rank and transfers thereto 26 species. The same author (*ibid.* **13**:545–550. 1915) in an article entitled "Neue Gattungen und Arten der Cynoglosseae" describes several species new to science and characterizes two new genera, namely *Adelocaryum* from India and Central Asia, and *Bilegnum*, which is based on *Mattia Bungei* Boiss., from Persia.—T. S. BRANDEGEE (Univ. Calif. Pub. Botany **6**:177–197. 1915) in a 7th article under the caption "Plantae mexicanae Purpusianae" has published 61 new species of flowering plants, mainly from Chiapas and Oaxaca.—N. L. BRITTON (Ann. Mo. Bot. Gard. **2**:33–58. *pls. 1, 2.* 1915) gives a brief account of the vegetation of Mona and Desecheo islands, which lie between Porto Rico and Santo Domingo, and estimates that the total land flora of the former consists of as high as 500 species and of the latter of at least 200 species. A partial list of the plants collected on Mona Island is appended. New species are recorded in *Pedilanthus, Tabebuia,* and *Riccia.* One new genus (*Mallotonia*) is proposed, which is based on *Tournefortia gnaphalodes* R. Br. The same author (Bull. Torr. Bot. Club **42**:365–392. 1915) under the general title "Studies of West Indian plants VI" includes a synoptical revison of the genus

Notable among his paleobotanical studies are those on Cycadofilicales, Bennettitales, Coniferales, etc. In the first group he described an interesting new genus *Mittagia* (resembling *Lagenostoma*), characterized by megasporangia not solitary but in sori, and also by the presence of 4 functional megaspores in each megasporangium.

The author's studies on the fossil floras of Normandy are of importance. In dealing with fossil conifers he did not make the mistake of certain German and English anatomists, in regarding rays as of paramount diagnostic significance. A supposed palm leaf *Propalmophyllum liasanum*, described by our author from the Lias, is according to ZEILLER of very problematical value. From the same geological level LIGNIER described remains of Cordaitales and Calamodendreae, a much later occurrence of these ancient types than has hitherto been recorded.

Important anatomical results reached by the author independently of, but in conformity with, workers on this side of the Atlantic were the conclusion that the herbaceous is derived from the woody type of stem, and that leaves are of great importance in the evolutionary history of plants. He divided vascular plants on the basis of the morphology of the leaf into Phylloideae and Phyllineae. The Phylloideae represent the Lycopsida, with the Equisetales and Sphenophyllales left out. The Phyllineae correspond to the Pteropsida, with the Equisetales and Sphenophyllales added (under the caption of Articulatae). SCOTT has further added to the latter the Psilotaceae and erected them into the phylum Sphenopsida.

LIGNIER's activities were so numerous and important that it is impossible to do justice to them here. Botanical evolution has suffered a great loss in his death.—E. C. JEFFREY, *Harvard University*.

CURRENT LITERATURE

NOTES FOR STUDENTS

Current taxonomic literature.—B. BALFOUR and W. W. SMITH (Notes Roy. Bot. Gard. Edin. **9**:63, 64. *pl. 148*. 1915) describe and illustrate a new genus (*Beesia*) of the Ranunculaceae from northern Burma and Yunnan, China. —R. BENOIST (Not. Syst. **3**:176–180. 1915) has published 6 new species of *Qualea* and *Lecythis* from South America.—E. P. BICKNELL (Bull. Torr. Bot. Club **42**:549–570. 1915) in the 16th article on the "Ferns and flowering plants of Nantucket" enumerates the Compositae and describes a new golden-rod (*Solidago aestivalis*).—S. F. BLAKE (Jour. Bot. **53**:56–58, 103–104, 135–137, 153–158, 193–202, 225–235, 306–307, 322–324. 1915) has published a "Revision of *Salmea* and allied genera," describes new speceis in *Amaranthus*, *Heterosperma*, *Notoptera*, *Otopappus*, *Perymenium*, *Verbesina*, and *Zexmenia* from Mexico, Central and South America, and includes also a new genus (*Steiractinia*) of the Compositae to which 6 species are referred, all being indigenous to northern South America. The same author (Kew Bull. 348. 1915) has published a new genus (*Stenocarpha*) of the Compositae from Mexico.—F. BÖDEKER (Monats. für Kakteenkunde **25**:76–80. 1915) describes and illustrates a new species of *Mamillaria* (*M. multihamata*) from Mexico.—A. BRAND (Rep. Sp. Nov. **14**:146–156. 1915) under the title "Neue Borraginaceen Studien" describes several new species and raises the section *Mattiastrum* Boissier of *Paracaryum* to generic rank and transfers thereto 26 species. The same author (*ibid.* **13**:545–550. 1915) in an article entitled "Neue Gattungen und Arten der Cynoglosseae" describes several species new to science and characterizes two new genera, namely *Adelocaryum* from India and Central Asia, and *Bilegnum*, which is based on *Mattia Bungei* Boiss., from Persia.—T. S. BRANDEGEE (Univ. Calif. Pub. Botany **6**:177–197. 1915) in a 7th article under the caption "Plantae mexicanae Purpusianae" has published 61 new species of flowering plants, mainly from Chiapas and Oaxaca.—N. L. BRITTON (Ann. Mo. Bot. Gard. **2**:33–58. *pls. 1, 2*. 1915) gives a brief account of the vegetation of Mona and Desecheo islands, which lie between Porto Rico and Santo Domingo, and estimates that the total land flora of the former consists of as high as 500 species and of the latter of at least 200 species. A partial list of the plants collected on Mona Island is appended. New species are recorded in *Pedilanthus*, *Tabebuia*, and *Riccia*. One new genus (*Mallotonia*) is proposed, which is based on *Tournefortia gnaphalodes* R. Br. The same author (Bull. Torr. Bot. Club **42**:365–392. 1915) under the general title "Studies of West Indian plants VI" includes a synoptical revison of the genus

Coccolobis in Cuba, recognizing 23 species of which 6 are new to science; a revision of *Anastraphia* with 21 species and 12 new; 14 new species are added to *Tabebuia;* and 12 new species are recorded in various genera of flowering plants. In a 7th article of the same series (*ibid.* 487–517) are included synoptical revisions of the Cuban *Scleria* with 28 species of which 4 are new, of *Tricera* with 18 species of which 9 are new, of *Plumiera* with 9 species of which 5 are new, of *Guettarda* with 26 species of which 7 are new; additional new species are described in *Badiera*, *Coccolobis*, *Portulaca*, *Chamaecrista*, *Rhamnidium*, *Nashia*, and *Exostema*.—V. F. BROTHERUS and S. OKAMURA (Bot. Mag. Tokyo **29**:186–188. *pl. 8.* 1915) describe and illustrate a new genus of moss (*Ishibaea*) from Japan. The genus is dedicated to EKICHI ISHIBA, a noted Japanese bryologist.—F. BUBÁK and H. SYDOW (Ann. Mycol. **13**:7–12. 1915) under the title "Einige neue Pilze" have published several new species of fungi including a new genus (*Pachybasidiella*) found on leaves of *Acer dasycarpa*.—L. BUSCALIONI and G. MUSCATELLO (Malpighia **27**:127–190. 1915–1916) in continuation of their studies of the genus *Saurauia* have published two new species from Costa Rica.—A. H. CHIVERS (Mem. Torr. Bot. Club **14**:155–240. *pls. 6–17.* 1915) has published a "Monograph of the genera *Chetomium* and *Ascotricha*," recognizing 28 species of the former genus and 2 of the latter.—E. CHIOVENDA (Annali di Botanica **13**:371–410. 1915) under the title "Plantae novae vel minus notae e Regione Aethiopica" describes several species and proposes the following new genera: *Afrotrichloris* of the Gramineae and *Peltophoropsis* of the Leguminosae.—R. CHODAT (Bull. Soc. Bot. Genève II. **7**:65, 66. 1915) has published a new species of *Prosopanche* (*P. clavata*) from South America.—O. F. COOK (Jour. Wash. Acad. Sci. **5**:236–241. 1915) has proposed two new genera: *Glaucothea*, based on *Brahea armata* Wats. of northern Lower California, and *Styloma*, based on *Pritchardia pacifica* Seem. and Wendl. a palm of the Fiji Islands. The same author (*ibid.* 287–289) characterizes a new genus (*Tribroma*), based on *Theobroma bicolor* Humb. and Bonpl.—A. DAVIDSON (Bull. S. Cal. Acad. Sci. **14**:11, 12. 1915) has described two new species of *Calochortus* (*C. discolor* and *C. campestris*) from California. K. DOMIN (Bibl. Botanica, Heft 85^{iv}. 401–551. *pls. 14–18.* 1915) in continuation of his studies on the flora and plant geography of Australia has published upward of 50 new species and varieties of monocotyledonous plants and describes a new genus (*Queenslandiella*) of the Gramineae.—H. A. EDSON (Jour. Agric. Research **4**:279–291. *pls. 44–48.* 1915) gives an account of a new fungus disease of sugar beets and radishes for which he proposes the generic and specific name *Rheosporangium aphanidermatus*.—A. D. E. ELMER (Leafl. Philipp. Bot. **7–8**:2543–2919. 1915) has described 248 new species of flowering plants of the Philippine Islands. One new genus (*Quadrasia*) of the Flacourtiaceae is included.—A. ENGLER (Bot. Jahrb. **53**:9–274, 312–605. 1915) in cooperation with several specialists has published the 44th and 45th articles of the series "Beiträge zur Flora von Afrika." Approximately 440 species new to science are recorded, and 3 new genera are proposed, namely,

Synandrodaphne Gilg of the Thymelaeaceae, *Centrostigma* and *Stolzia* Schltr. of the Orchidaceae.—A. W. EVANS (Bull. Torr. Bot. Club **42**:259–308. 1915) presents a discussion of the genus *Plagiochasma* in North America. Six species are recognized, one of which (*P. Landii*) from Mexico is new to science. —O. A. FARWELL (*ibid.* 247–257. *pls. 12–18.* 1915) presents a paper on the genus *Polygonatum* in Michigan; 5 species and several varieties are recognized. —R. G. FRAGOSO (Bot. Soc. Esp. Hist. Nat. **15**:120–132. 1915) under the title "Hongos parásitos de la florula hispalense, nuevos ó poco conocidos" describes several species of fungi and includes a new genus (*Septoriopsis* Fragoso and Paul) which is parasitic on citrus fruits.—F. GAGNEPAIN (Not. Syst **3**:180–192. 1915) under the title "Papilionacées nouvelles ou critiques" has published several species new to science and describes the following new genera: *Antheroporum*, *Diphyllarium*, and *Endomallus* from China.— H. M. HALL (Univ. Calif. Publ. Bot. **6**:165–176. *pl. 20.* 1915) has published 7 new species of flowering plants from California and records important data on other species occurring in the state.—H. HARMS (Rep. Sp. Nov. **13**:523–527. 1915) has published 2 new species of *Prosopis* from Paraguay and 7 new species of *Inga* from Central and South America.—E. HASSLER (Rep. Sp. Nov. **14**:157–159. 1915) describes a new species of *Zexmenia* from Argentina and transfers two additional species to this genus from *Verbesina*. The same author (*ibid.* 161–180) has published several new species and varieties of flowering plants from Paraguay.—L. HAUMAN (Anal. Mus. Nac. Hist. Nat. Buenos Aires **27**:285–306. 1915) under the title "Note sur les Joncacées des petits genres Andins" describes and illustrates a new genus *Andesia*, based on *Oxychloe bisexualis* Kuntze. The same author (*ibid.* 441–516) gives a synoptical revision of the Dioscoreaceae of Argentina, describing and illustrating several new species and varieties.—B. HAYATA (Tokyo Bot. Mag. **29**:31–34. 1915) has proposed a new genus (*Pseudixus*), based on *Viscum japonicum* Thunb.—T. HERZOG (Mededeelingen Rijks Herb. no. 27. pp. 1–00. 1914–1915) in cooperation with several specialists records the plants collected by Dr. TH. HERZOG in Bolivia during the years 1910 and 1911. Upward of 60 species new to science are described, and one new genus (*Eleutherostemon*) of the Ericaceae is included.—A. S. HITCHCOCK (Am. Jour. Bot. **2**:290–310. 1915) under the title "New or noteworthy grasses" records important data concerning a number of species, makes several new combinations, and describes 7 species new to science.—A. S. HITCHCOCK and A. CHASE (Contrib. U.S. Nat. Herb. **17**:450–539. 1915) under the title "Tropical North American species of *Panicum*" have published an important contribution to our knowledge of this genus supplementing their recent revision of the group. In the present paper the authors recognize 116 species and 3 subspecies; and of these, 9 species are new to science. A valuable factor in this paper is the introduction of an outline map on which the geographical distribution of each species is indicated.—H. D. HOUSE (N.Y. State Mus. Bull. 176. p. 38. 1915) describes a new species of *Physostegia* (*P. latidens*) from

near Utica, New York.—F. T. HUBBARD (Am. Jour. Bot. **2**:169–198. 1915) presents the results of a "Taxonomic study of *Setaria italica* and its immediate allies." Several new varieties, forms, and combinations are proposed.—A. HUE (Bull. Soc. Bot. France **15**:13–23. 1915) in an article entitled "Tribus Umbilicariacearum genera exposuit" characterizes a new genus (*Charcotia*), based on *Umbilicaria rufidula* Hue.—S. ITO (Bot. Mag. Tokyo **29**:15–22. *pl. 1.* 1915) describes and illustrates a new genus (*Typhulochaeta*) of the Erysiphaceae.—E. KOEHNE (Bot. Jahrb. **52**:277, 278. 1915) has published two new species of *Amelanchier* from western North America. The same author (*ibid.* 279–333) describes upward of 30 new species and varieties of *Prunus*, and (*ibid.* 334–345) records 8 species of *Pygeum* new to science.—B. KOSO-POLIANSKY (Jour. Russe Bot. 1915. pp. 1–21) under the title "A revision of the oriental genus *Grammosciadium* DC." recharacterizes this genus and proposes the following related genera: *Stenodiptera*, *Golenkinianthe*, and *Chrysophaë*.—F. KRÄNZLIN (Arkiv för Botanik **14**:no. 10. pp. 1–8. 1915) has published 7 new species of orchids from Mexico and Brazil.—I. M. LEWIS (Bull. Univ. Texas. no. 22, pp. 1–169. 1915) has recently published a small volume entitled "The trees of Texas: an illustrated manual of the native and introduced trees of the state."—TH. LOESENER (Rep. Sp. Nov. **14**:97–113. 1915) in a 5th article in the series "Mexikanische und zentralamerikanische Novitäten" in cooperation with several specialists records further collections of flowering plants made in Mexico mainly by RUDOLF ENDLICH. A new species and a new variety are described in *Plantago*.—J. LUNELL (Am. Mid. Nat. **4**:152–165. 1915) begins an enumeration of the vascular plants of North Dakota. One new variety of *Alisma* is characterized.—B. LYNGE (Arkiv för Botanik **13**:no. 13. pp. 1–172. *pls. 1–5.* 1914) under the title "Die Flechten der ersten Regnellischen Expedition" characterizes a new genus (*Pseudoparmelia*) and gives a synopsis of *Parmelia*, adding several new species to the latter genus.—K. K. MACKENZIE (Bull. Torr. Bot. Club **42**:405–422. 1915) in continuation of his studies in the genus *Carex* records a new species (*C. egregia*) from northern United States. The same author (Smiths. Misc. Coll. **65**:no. 7. pp. 1–3. 1915) describes two new species of *Carex* from the southwestern United States.—T. MAKINO (Bot. Mag. Tokyo **29**:279–283. 1915) proposes two new genera (*Matsumurella* and *Ajugoides*) of the Labiatae from Japan.—O. MATTIROLO (Mem. Accad. R. Scienze Torino II. **63**:213–218. 1912) has described and illustrated a new genus (*Jaczewskia*) of the Hysterangiaceae.—A. MAUBLANC and E. RANGEL (Bol. Agr. São Paulo, sér XVI. pp. 310–328. *pls. 4–9.* 1915) under the title "Alguns fungos do Brasil, novos ou mal conhecidos" have published several new species of fungi and propose three new genera, namely *Chaetolentomita* of the Pyrenomycetes, *Leandria* and *Didymothozetia* of the Hyphomycetes.—W. R. MAXON (Bull. Torr. Bot. Club **42**: 79–86. 1915) has published a synoptical revision of the North American species of *Psilogramme*, recognizing 8 species of which 3 are new to science. The same author (Smiths. Misc. Coll. **65**:no. 8. pp. 1–12. 1915) presents a "Report

upon a collection of ferns from western South America" and includes the descriptions of 6 new species.—E. D. MERRILL (Philipp. Jour. Sci. **10**:1–84. 1915) in the 11th paper in the series entitled "New or noteworthy Philippine plants" has described about 90 species of flowering plants; and (*ibid.* 99–144) in continuation of his studies of the Rubiaceae of the Philippine Islands has published 42 new species in various genera of this family; and (*ibid.* 195–225) 12 new species of *Schefflera* and 22 of *Eugenia* are described from the Philippine Islands; and (*ibid.* 227–264) under the title "Studies on Philippine Anonaceae I" he records 70 species of this family of which 25 are described as new to science. Two new genera are proposed, namely *Griffithianthus* and *Guamia;* and (*ibid.* 265–285) under the caption "Plantae Wenzelianae III" 21 new species of flowering plants are recorded and one new genus (*Wenzelia*) of the Rutaceae is proposed. These are based primarily on plants collected in Leyte by Mr. C. A. WENZEL; and (*ibid.* 287–349) in continuation of his researches on the Philippine flora he has published 63 new species and several varieties of flowering plants. The same author (Jour. Wash. Acad. Sci. **5**:530–542. 1915) has taken up the generic name *Nauclea* L. and transferred thereto certain species hitherto referred to *Sarcocephalus.* A new generic name (*Neonauclea*) is proposed for *Nauclea* of KORTHALS and subsequent authors, and to *Neonauclea* the author transfers about 50 species.—G. MOESZ (Bot. Közlemények **14**:145–158. 1915) under the title "Mykologiai Közlemények" describes several new species of fungi and characterizes a new genus (*Chaetosphaeronema*), based on *Sphaeronema hispidulum* Corda.—A. M. MOSS (Jour. Bot. **53**:1–8. *pl. 535.* 1915) in an article entitled "The Aristolochias of Pará (Brazil)" includes descriptions of 4 new species of this genus by SPENCER MOORE.—J. A. NIEUWLAND (Am. Mid. Nat. **4**:89–95. 1915) has proposed two new genera, namely *Apetlorhamnus* and *Litanum.*—V. NORLIND (Arkiv för Botanik **14**:no. 6. pp. 1–18. *pls. 1–4.* 1915) has published 8 new species of *Oxalis* from South America.—C. H. OSTENFELD (Bull. Torr. Bot. Club **42**: 659–662. *pl. 32.* 1915) describes and illustrates a new species of *Ruppia* (*R. anomala*) from Porto Rico.—N. PATOUILLARD (Philip. Jour. Bot. **10**:85–98. 1915) under the heading "Champignons des Philippines communiques" has published several new species and includes one new genus, namely *Duportiella.*—R. PILGER (Notizblatt Königl. Bot. Gart. u. Mus. Berlin-Dahlem **6**:261–310. 1915) under the general title "Plantae Uleanae" in cooperation with several specialists has published upward of 60 new species and varieties of flowering plants based on the collections of E. ULE in South America. The same author (*ibid.* 311–396) has published approximately 75 species new to science. The following new genera are included: *Abutilothamnus, Codonochlamys,* and *Triplochlamys* Ulbrich of the Malvaceae, and *Microbignonia* Kränzl. of the Bignoniaceae.—H. PITTIER (Jour. Wash. Acad. Sci. **5**:468–474. 1915) has published 4 new species of leguminous trees from Panama.—E. L. REED (Torreya **15**:246, 247. 1915) describes a new species of sundew (*Drosera annua*) from Texas.—A. REHDER (Proc. Amer. Acad. **50**:225–241. 1915)

presents a "Synopsis of the Chinese species of *Pyrus*" in which 12 species are recognized, 6 being new to science.—J. F. ROCK (Bull. Torr. Bot. Club **42**:77, 78. *pl. 8*. 1915) describes and illustrates a new species of *Cyanea* (*C. Larrisonii*) from the Hawaiian Islands.—R. A. ROLFE (Curtis' Bot. Mag. *pl. 8635*. 1915) describes and illustrates a new orchid (*Sievekingia Shepheardii*) from Colombia.—E. ROSENSTOCK (Hedwigia **56**:355–371. 1915) under the title "Filices brasilienses novae" has published 29 new species and varieties of ferns. —W. ROTHE (Bot. Jahrb. **52**:355–434. 1915) presents a revision of the genus *Marsdenia* recognizing 47 species of which 9 are new to science.—P. A. SACCARDO (Annal. Mycol. **13**:115–138. 1915) under the title "Notae mycologicae" describes new species of fungi from North America, Philippine Islands, etc., and includes a new genus (*Heteroceras*) found on dead leaves of *Tilia europaea*. —W. E. SAFFORD (Jour. Wash. Acad. Sci. **5**:355–360. 1915) has described 3 new species of bullhorn acacias from Mexico.—R. SCHLECHTER (Rep. Sp. Nov. **13**:537–544, 554–566. 1915) under the caption "Asclepiadaceae Philippinenses" has published 37 new species and proposes the following new genera: *Clemensia*, *Clemensiella*, *Dolichostegia*, and *Petalonema;* and (*ibid.* **14**:114–133. 1915) has described 40 new species of orchids from Ecuador, based on collections made by A. SODIRO and by L. MILLE. The same author (Orchis **9**:4–9, 17–20, 49–54, 90–96. 1915) has published several new species of orchids from Mexico, Central and South America, and includes a new genus (*Jainiopsis*) from India.—H. SCHINZ (Vierteljahrschr. Zürich Naturf. Gesells. **60**:389–422. 1915) under the title "Beiträge zur Kenntnis der afrikanischen Flora xxvi" in cooperation with the specialists F. KRÄNZLIN and A. THELLUNG has published several new species of flowering plants and includes the following new genera: *Manulcopsis* Thell. of the Scrophulariaeceae and *Dinteracanthus* C. B. Clarke of the Acanthaceae. The same author (*ibid.* 423–432) records 10 new species of flowering plants, 7 of which are from Mexico and South America.—W. A. SETCHELL (Univ. Calif. Publ. Bot. **6**:79–152. *pls. 10–16*. 1914) in an article entitled "The *Scinaia* assemblage" presents the results of a detailed study of the genus *Scinaia* and its near allies. Several new species are described and one new genus (*Pseudoscinaia*) is characterized.—C. SPEGAZZINI (Anal. Mus. Nac. Hist. Nat. Buenos Aires **27**:37–74. 1915) under the title "Segunda contribución al conocimiento de las Laboulbeniales Italianas" has published upward of 30 new species and proposes the following new genera: *Parahydraeomyces* and *Thripomyces*.—P. C. STANDLEY (Jour. Wash. Acad. Sci. **5**:57–59. 1915) describes a new genus (*Zuckia*) of the Chenopodiaceae from Arizona; and (*ibid.* 72–76, 391–396) presents the results of studies in the Amaranthaceae, reinstates *Centrostachys* Wallich, records new combinations in this genus as well as in *Iresine*, *Lagrezia*, and *Lithophila*. The same author (*ibid.* 600–602) describes a new species of *Geranium* (*G. Jahnii*) from Venezuela. —O. STAPF (Hook. Ic. *pl. 3033*. 1915) describes and illustrates a new genus (*Homozeugos*) of Gramineae from west tropical Africa.—G. K. SUTHERLAND (Trans. Brit. Myc. Soc. **5**:147–155. *pl. 3*. 1915) under the title "New marine

Pyrenomycetes" describes and illustrates two new genera, namely *Trailia* and *Orcadia*, both parasitic on the thallus of *Ascophyllum* and found along the shores of the Orkney Islands.—W. T. SWINGLE (Jour. Wash. Acad. Sci. **5**:165–176. 1915) has published an interesting article dealing with the kumquat oranges and describes a new genus (*Fortunella*) based on *Citrus margarita* Lour. Four species, all apparently originating from China, are referred to the new genus and they promise to be of considerable economic value in breeding citrus fruits. The same author (*ibid.* 569–578) records another new genus (*Microcitrus*) of citrus fruits, based on *Citrus australasica* F. Muell. Four species are recognized, all being natives of Australia.—H. and P. SYDOW (Ann. Mycol. **13**:35–43. 1915) under the heading of "Novae fungorum species XIII" include descriptions of two new genera, namely *Myelosperma* found on leaves of *Cocos nucifera* at Peradeniya and *Cheiropodium* found in Japan on leaves of *Carex breviculmis*.—R. THAXTER (Proc. Amer. Acad. **51**:1–51. 1915) under the title "New Indo-Malayan Laboulbeniales" has described 46 species new to science and proposes a new genus, namely *Tettigomyces*.—F. THEISSEN and H. SYDOW (Ann. Mycol. **13**:149–746. *pls. 1–6*. 1915) in a monographic study of the *Dothideales* have characterized the following new genera: *Achorella*, *Agostaea*, *Amerodothis*, *Anisochora*, *Armatella*, *Bagnisiopsis*, *Camarotella*, *Catabotrys*, *Catacaumella*, *Coccodothella*, *Crotone*, *Dibotryon*, *Dictyochorella*, *Dictyodothis*, *Dothidina*, *Elmerococcum*, *Endodothella*, *Englerodothis*, *Epibotrys*, *Haplothecium*, *Hyalocurreya*, *Hysterostomina*, *Inocyclus*, *Isomunkia*, *Leveillella*, *Leveillina*, *Metameris*, *Monopus*, *Monorhiza*, *Monorhizina*, *Munkiodothis*, *Omphalospora*, *Ophiocarpella*, *Pachypatella*, *Phaeocorella*, *Phaeotrabutiella*, *Phragmocarpella*, *Phragmocauma*, *Phragmodothella*, *Polycyclina*, *Rhopographina*, *Rosenscheldiella*, *Scirrhiachora*, *Scirrhophragma*, *Scirrhodothis*, *Septomazzantia*, *Symphaster*, *Syncarpella*, *Thyriopsis*, *Trichochora*, and *Ulcodothis*. Many new species are described.—E. N. TRANSEAU (Ohio Jour. Sci. **16**:17–31. 1915) under the title "Notes on the Zygnemales" has published 9 species and 2 varieties new to science.—W. TRELEASE (Trans. Acad. Sci. St. Louis **23**:129–152. *pls. 6–35*. 1915) in a paper entitles "The Agaveae of Guatemala" gives a synoptical revision of the agaves of Guatemala, recognizing 19 species of which 5 are described as new; also a revision of *Furcraea* with 5 species of which 4 are new.—W. B. TURRILL (Jour. Linn. Soc. **43**:15–39. 1915) under the title "A contribution to the flora of Fiji" enumerates 72 species of phanerogams, collected by Sir EVERARD IM THURN in 1905–1907. Of the species recorded 24 are new to science. One new genus (*Pareugenia*) of the Myrtaceae is proposed.—E. ULBRICH (Rep. Sp. Nov. **13**:498–518. 1915) has published several new species and varieties of the Malvaceae from South America.—I. URBAN (Rep. Sp. Nov. **13**:465–484. 1915) has published 24 species of flowering plants new to science from the West Indies. One new genus (*Selleophytum*) related to *Zinnia* is described.—M. VICTORIN (Ottawa Nat. **28**:155–160. 1915) describes and illustrates a new aster (*Aster linariifolius* var. *Victorinii* Fernald) from Quebec.—H. F. WERNHAM (Jour. Bot. **53**:15. 1915) records a new species of the recently

established genus *Tournefortiopsis* from South America.—F. v. WETTSTEIN (Oesterr. Bot. Zeitschr. **65**:145–156. *pls. 3, 4.* 1915) gives an account of an alga found in Kremsmünster, upper Austria, identifying it with *Botrydium pyriforme* Ktz., for which he proposes the generic name *Geosiphon*.—R. S. WILLIAMS (Bull. Torr. Bot. Club **42**:393–404. *pls. 21–25.* 1915) in an article entitled "Mosses from the west coast of South America" describes several new species and records a new genus (*Pseudocrossidium*).—J. C. WILLIS (Jour. Linn. Soc. **43**:49–54. 1915) in continuation of his studies on the Podostemaceae, particularly in the light of material from Brazil, has proposed a new family (Tristichaceae) to include *Tristicha*, *Lawia*, and *Weddellina*.—N. WORONICHIN (Bull. App. Bot. **8**:769–807. *pls. 134–136.* 1915) has published several new species of fungi, including also a description of a new genus, namely *Antennulariella*.—A. ZAHLBRUCKNER (Rep. Sp. Nov. **13**:528–537. 1915) has published 13 new species of *Burmeistera* and *Centropogon* from Ecuador and Colombia. The same author (*ibid.* **14**:133–142. 1915) records 21 additional new species of Lobeliaceae from South America.—J. M. GREENMAN.

Botanical researches of the Carnegie Institution.—The annual report[1] of the year 1915 affords a brief review of the varied lines of botanical research in progress at the Desert Laboratory and elsewhere under the general direction of the Carnegie Institution. It also announces the report of investigations that are now being published, or that are to appear in the near future. Only a few of the more prominent lines of investigation can be noted here, and among them none is more important than the group of problems relating to the conditions of plant growth, especially in relation to soil aeration and temperature, as well as to the processes of respiration and photosynthesis, by MACDOUGAL, LIVINGSTON, CANNON, SPOEHR, and their associates. Studies upon succulents are being continued by MACDOUGAL, LANG, and BROWN; while the special water relations of plants have engaged the attention of LIVINGSTON in an improved form of atmometer and in some transpiration studies. This latter field has also been worked by BAKKE and SHREVE, using the method of standardized hygrometric paper.

Among the more important lines of phytogeographic research are investigations of osmotic pressure of cell sap in relation to environmental conditions by HARRIS, of the vegetation of Arizona mountains by SHREVE, and of climatic cycles and successions by CLEMENTS. The investigations of various root systems by CANNON, of the Salton Sea region by a corps of workers, and of the relationships of the Cactaceae by BRITTON and ROSE are being continued. There have been also climatic studies by HUNTINGTON, and genetic analyses by LLOYD, MACCALLUM, and TOWER.—GEO. D. FULLER.

[1] MACDOUGAL, D. T., Annual report of the director of the department of botanical research. Carnegie Inst. Washington Year Book no. 14 for 1915. pp. 55–106. 1916.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

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